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THE SPRING AND SUMMER DISPERSION OF MALE  
FRANKLIN'S GROUSE IN LODGEPOLE PINE FOREST  
IN SOUTHWESTERN ALBERTA

by



RODERICK ARCHIBALD McLACHLIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read,  
and recommend to the Faculty of Graduate Studies for  
acceptance, a thesis entitled "The spring and summer  
dispersion of male Franklin's grouse in lodgepole pine  
forest in southwestern Alberta" submitted by Roderick  
Archibald McLachlin in partial fulfilment of the  
requirements for the degree of Master of Science.



## ABSTRACT

The spring and summer dispersion of male Franklin's grouse (Canachites canadensis franklinii) was studied on a 600 ha study area in the high foothills of southwestern Alberta from 1965 to 1968.

The population and its age composition were thought to be fairly constant throughout the study, averaging 4.3 adults and 2.3 yearlings per square km in 1967 and 1968. Over the period of the study, survival was 68 percent for yearlings and 77 percent for adults.

All adults and some yearlings occupied home ranges during the spring and summer, while other yearlings appeared to wander, some apparently adopting home ranges over the summer. Home ranges of adults and yearlings averaged 2.1 and 3.4 ha respectively. Adults were more localized on their home ranges during the breeding period, particularly in the evening when they occupied small display areas. Older adults did not generally change home ranges and vacancies were usually filled by younger birds. Territoriality, shown for adults and suggested for some yearlings, was thought to function in spacing males.

Males utilized only 28 percent of the lodgepole





pine (Pinus contorta) forest of the study area for their home ranges. As this occupied area had greater overstory cover, lower middlestory cover, greater stem density and canopy height and lower slope of the forest floor than in the lodgepole pine forest of the study area generally, habitat availability and selection were thought to affect dispersion of males. Adults utilized habitat of greater overstory cover and lower middlestory cover while localized yearlings utilized habitat of greater middle-story cover than in the areas occupied by home ranges generally. Adults appeared to utilize more open habitat for their display areas than that over the rest of their home ranges. When compared to the habitat utilized during the breeding period, adult males utilized habitat of greater middlestory cover during the moult. Adult males were found to utilize habitat of greater overstory cover and lower middlestory cover than that utilized by females.



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## INTRODUCTION

Spruce grouse (Canachites canadensis) were classified by Aldrich (1963) into four subspecies. These are: Hudsonian spruce grouse (C.c. canadensis) which occupies the boreal forest from Labrador to Alaska; Canada spruce grouse (C.c. canace) of the hardwood-conifer forest of the St. Lawrence basin; Valdez spruce grouse (C.c. artratus) which inhabits the Pacific rain forests of Alaska; and Franklin's spruce grouse (C.c. franklinii), the subject of this study, which inhabits the montane forests of the northern Rocky Mountains and the Cascades.

Hammerstrom and Hammerstrom (1963) stated that, at that time, less literature was available for spruce grouse than for any other North American grouse. While more literature is now available, little of it deals with the problem of dispersion. Only Stoneberg (1967), Ellison (1968a), Robinson (1969) and McCourt (1969), deal directly with dispersion. Others, Lumsden (1961) and MacDonald (1968) on behavior, Zwickel and Martinsen (1967) and Ellison (1968b) on age determination, and Lumsden and Weeden (1963) on harvest, are of less assistance to this study. Hopefully, my work will add to the steadily growing body of knowledge



on spruce grouse, and in particular, on Franklin's grouse.

The term "dispersion" as used in this study, is that of Wynne-Edwards (1962, p.1): "the placement of individuals or groups within the habitats they occupy, and the processes by which this is brought about". Thus, the study of dispersion can be divided into two central questions: "What is the placement of individuals or groups?", and "Why are they placed in this way?"

I attempted to answer these two questions for the male portion of a population of Franklin's grouse near the R.B. Miller Biological Station in southwestern Alberta during the springs and summers (1 May to 15 September) 1965 to 1968.



## METHODS AND MATERIALS

### General methods and materials

This study of male Franklin's grouse was done in conjunction with a study by K.H. McCourt on females of the same population (Mccourt, 1969). In this thesis the words "males" and "birds" will refer to male Franklin's grouse, unless otherwise stated.

Franklin's grouse are difficult to find, about 7.5 hours of search being required for each sighting of a male. Daily systematic searches of the study area by two to four workers were conducted to locate birds. Search entailed walking back and forth across sections of the study area, continually covering new ground in the manner in which fields might be cultivated, the whole area being searched every two to four days. I used a Labrador retriever throughout the study and in 1966 a German short-haired pointer. They did not add greatly to the productivity of search.

Birds were easily captured using an extensible noosing pole (Zwickel and Bendell, 1967), with no mortality resulting from this mode of capture. A minimum of recapturing was done so as to disturb the birds as little as





possible. Birds were marked with anodized aluminum leg bands: a coloured numbered band on the right leg, the colour of which distinguished the year of banding; and a distinctive combination of coloured, unnumbered bands on the left. Birds could easily be identified with field glasses at 10 m and left relatively undisturbed.

At each sighting a bird was identified and the date and time of day recorded. The location was noted from enlargements of aerial photos of a scale of 45 m to the cm overlaid with a 10 cm grid, and was recorded by the use of coordinates. Unbanded birds were captured and banded and their weights recorded to the nearest five g. Where possible, a central rectrix, a first primary and a central upper tail covert were taken from each bird for age determination.

#### Experimental methods and materials

Territorial behavior was investigated by examining the response of males to a mounted male Franklin's grouse with red plastic combs. Birds were transported from their points of capture in a light-proof sack and released to test territorial fidelity.

A tape-recording of a female call which was attractive to both males and females (MacDonald, 1968) was kindly provided by S.D. MacDonald in 1967. The call was transferred to a  $33\frac{1}{2}$  RPM record and a Herter's model 88



portable game caller was used to reproduce the call. The call was used in the search for males, particularly in areas where males were not found by conventional search.. It was also played at the boundaries of territories to investigate interactions of males. The call was also used in a census.

Three suitable parts of the study area were surveyed by compass and pace into a 200 m grid; during the census the call was played 15 minutes at each grid point and the birds which responded were recorded. The distances between grid points were believed close enough to allow any bird on the census area to hear the call. The populations of the census areas were also determined by conventional searching.

#### Methods of habitat measurement

Vegetation was measured at the point where each bird was sighted. Cover values described by Daubenmire (1959) were used to estimate the cover (maximum horizontal area enclosed by the true lateral outlines of the foliage) by individual species of plants and by all species combined. These values were estimated by eye and are as follows:

0 - absent

1 - present to 5%

2 - > 5% to 25%



3 - >25% to 50%

4 - >50% to 75%

5 - >75% to 95%

6 - >95% to 100%.

Two levels of cover were described in this manner. The overstory was considered to be composed of any tree higher than breast height (1.3 m), while any plant with winter buds higher than 0.25 m but less than breast height was considered to be middlestory. One exception was alder (Alnus crispa) which occasionally grew a little higher than breast height but always was considered as middle-story. The understory, composed of trees and shrubs shorter than 0.25 m and all other vegetation, was noted descriptively in field notes. Each analysis was done within a circle of 0.005 ha (50 square m). At the point where a bird was first seen, crossed strings were laid out as diameters (7.97 m) of the circle, and the extent of the circle was estimated from these diameters.

In early spring and late fall, the foliage of the deciduous species was often absent or incomplete. Therefore cover values of deciduous plants were always estimated as though summer foliage were present. Experience and the repeated analysis of 20 plots through the seasons showed that this could be done accurately.

Since Franklin's grouse show little tendency to





flush or run, I believe the vegetation analysed within these circles represents very closely the habitat utilized by the birds.

Vegetation analyses were also done at random points over the entire study area. Coordinates chosen from a table of random numbers were used to locate points on air photographs of the study area. On the study area, at each of these points, a stick was spun and I proceeded 25 paces in the direction of the small end of the stick. The point where my foot came down on the twenty-fifth pace was used as the centre of the plot. Analyses of the vegetation were done in the manner described above.

In addition, stem density, stem diameter, and canopy height were measured for the overstory in each of these random plots. Density was measured by counting the number of stems, by species and with all species combined. Diameters were measured at breast height in 2-cm-size-classes. An estimate of average canopy height and the slope across each plot was made by triangulation with an Abney level.

#### Confidence limits

The five per cent level of significance was chosen for the statistical treatment of the data for this study.





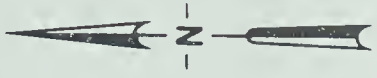
## RESULTS AND DISCUSSION

### THE STUDY AREA

The study area was located near the R.B. Miller Biological Station in the Bow River Forest Reserve in southwestern Alberta (Fig. 1). The total study area (1800 ha) was composed of a main study area (600 ha), on which intensive work was done, and an auxiliary study area (1200 ha), on which birds were banded to investigate movement on and off the main study area. The study began on a small part of the main study area, and, as we realized the necessity of working with a larger population, the area was increased through 1965 and 1966 to its full extent in the late summer of 1966. The main study area ranges from 1500 to 1900 m in altitude, and is probably best described as high foothill country (Fig. 2).

Most of the present vegetation of the Sheep River Valley has grown after the fires which swept the foothills during the 1920's and 1930's. On the main study area these fires were responsible for a lodgepole pine forest (Pinus contorta) of uniform age. Mixed forest of aspen (Populus tremuloides), balsam poplar (P. balsamifera), white spruce (Picea glauca), and lodgepole pine occurs on the southeast edge and in isolated areas of the study

Figure 1. Location of the study area near the R.B. Miller Biological  
Station, showing the extent of the main and auxiliary study  
areas.



ALBERTA



0 1 Km

ROAD

STREAM

MAIN STUDY AREA  
BOUNDARY

AUXILIARY STUDY AREA  
BOUNDARY

R.B. MILLER BIOLOGICAL  
STATION

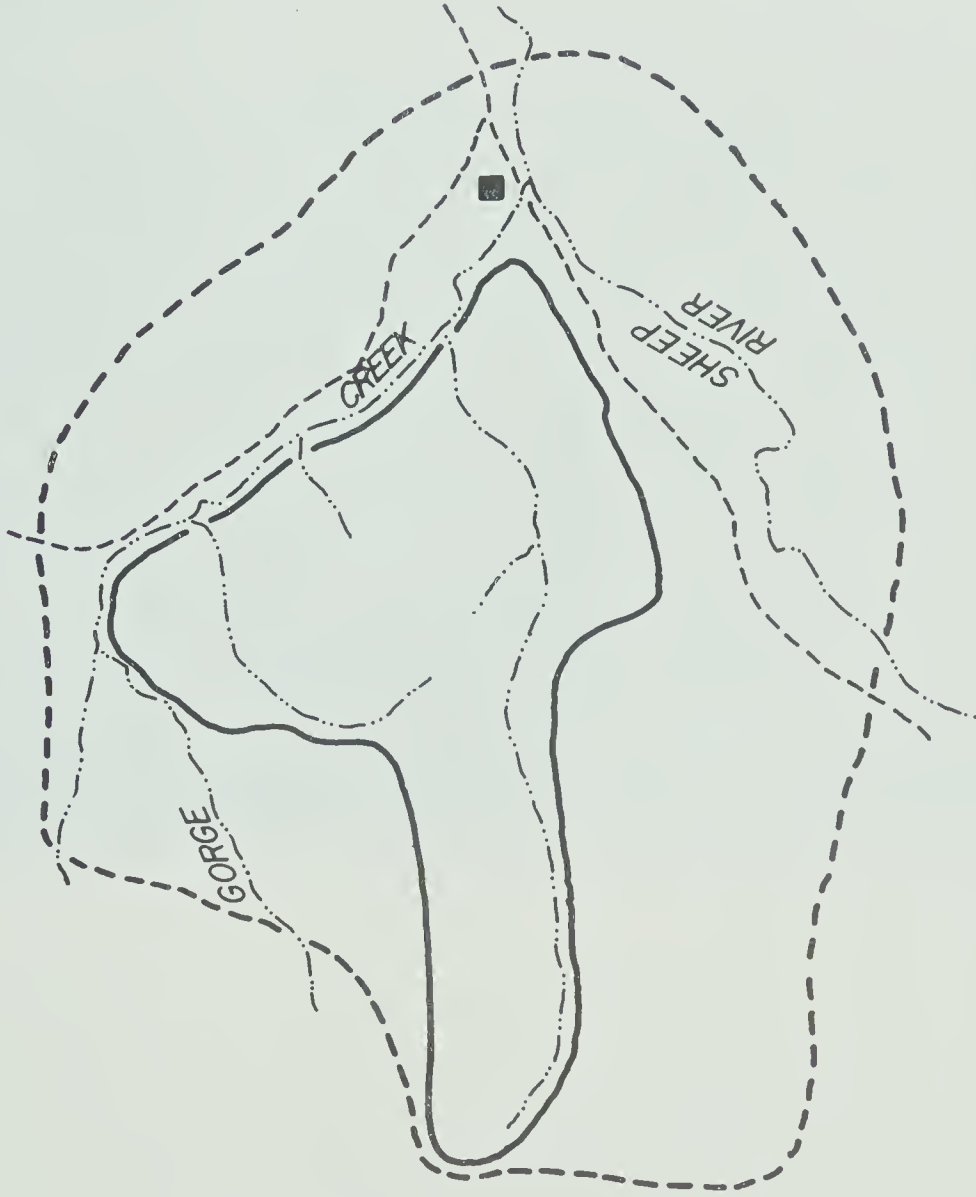


Figure 2. A view of the study area with the Rocky Mountains in the background (main study area outlined in white).





area. A few relict stands of white spruce survived the fires in the wet areas. There are also marshy areas, characterized by rushes (Juncus spp.), and meadows, characterized by rough fescue (Festuca scabrella). I classified the vegetation into four types: lodgepole pine forest, mixed forest, white spruce forest, and meadow and marsh. The distribution of these types was established from ground traverses and air photographs (Fig. 3). The proportion of each can be seen in Table 1.

Table 1. Proportion of each vegetation type on the main study area.

Vegetation type	Area(ha)	Percent of total area
White spruce forest	21	3.5
Meadow and marsh	45	7.5
Mixed forest	104	17.5
Lodgepole pine forest	429	71.5

#### Lodgepole pine forest

Overstory cover in the lodgepole pine forest (Table 2, original data in Appendix I) for all species combined occurred in 99 percent of the plots, the most important cover values being: two, at 30 percent; three,

Figure 3. The distribution of the four vegetation types  
on the main study area.



0 500 m



SPRUCE FOREST



MIXED FOREST



LODGEPOLE PINE FOREST



MEADOW AND MARSH



STREAM



STUDY AREA BOUNDARY

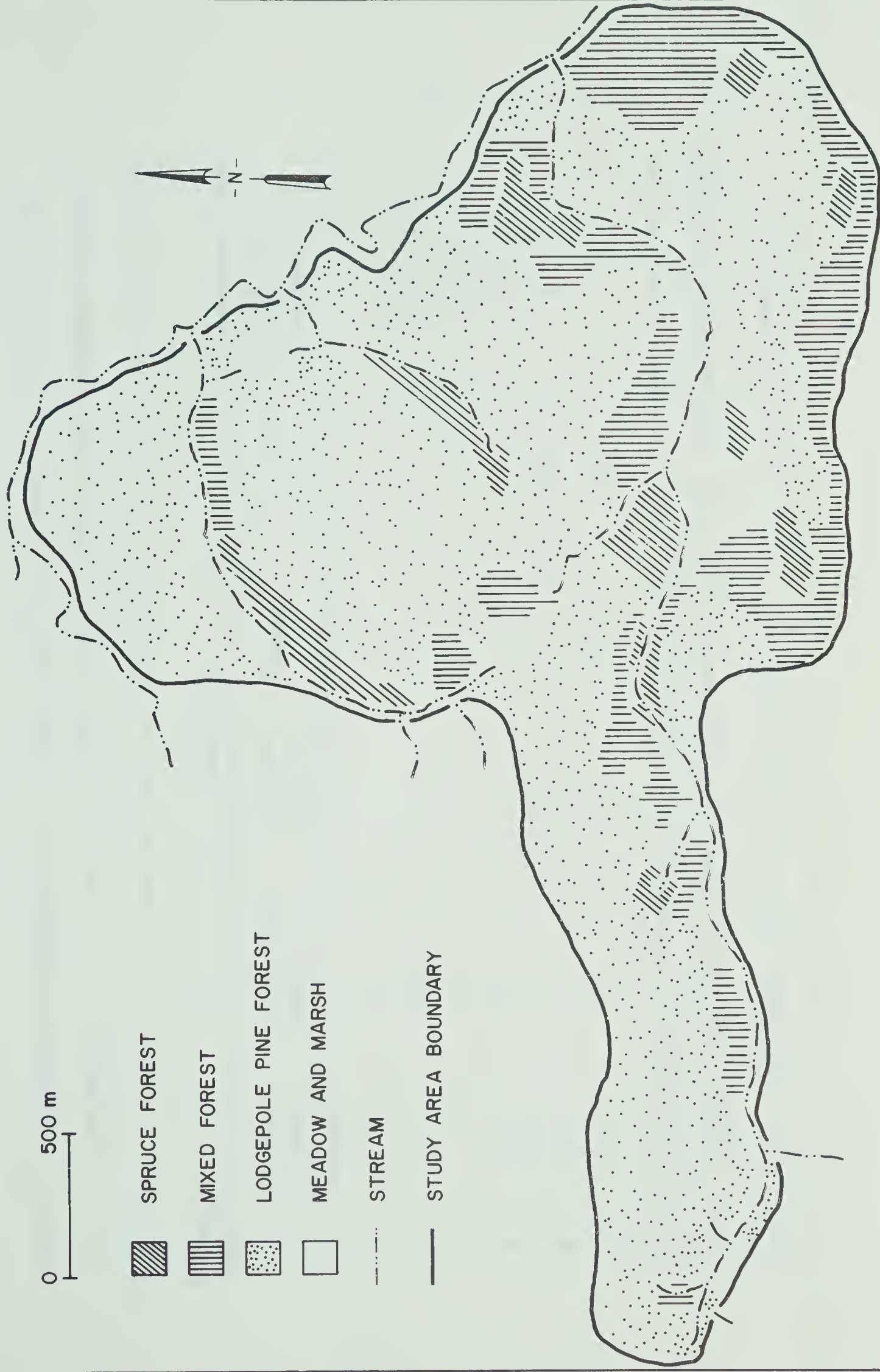
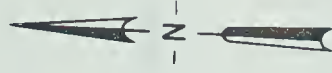




Table 2. Frequency distribution of cover values for species of plants in the overstory of the lodgepole pine forest (based on 225 random samples).

Cover value <sup>a</sup>	Species					Total for all species combined
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow	
5		1				2
4		19				23
3	1 <sup>b</sup>	41				40
2	13	31	1	1	1	30
1	39	7	2	1	24	4
0	47	1	97	98	75	1

<sup>a</sup>Cover values: 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent

<sup>b</sup>Percent of each cover value for each species and for all species combined.



at 40 percent; and four, at 23 percent. Lodgepole pine, the dominant species, its cover values very similar to those for all species combined, occurred in 99 percent of the plots, most commonly at a cover value of three. Other species contributed less to overstory cover. White spruce was present in 53 percent of the plots, usually at a cover value of one. Aspen and balsam poplar were present in a low percentage of the plots, usually at a cover value of one, while willow (Salix sp.) was present on 25 percent of the plots, also usually with a cover value of one.

Stem density (Table 3) for lodgepole pine on random plots, where present, averaged 19.4 per plot, while all species combined averaged 22.4 stems per plot. Lodgepole pine, 85.1 percent of the total stems, was dominant, averaging 3835 stems per ha, while spruce and willow were less numerous, averaging 298 and 364 stems per ha respectively. The poplars were present in very low numbers. Average total stem density for all species was 4514 stems per ha.

Stem diameters (dbh) for the overstory (Table 4) were larger for lodgepole pine than for the other species. Sixty-five percent of the lodgepole pine stems were greater than four cm in diameter, while 90 percent of the white spruce, 100 percent of the balsam poplar, 54 percent of the aspen and 98 percent of the willow were four cm or



Table 3. Stem density for species of plants in the overstory of the lodgepole pine forest (based on 225 random samples).

Density	Species				
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow
All species combined					
Stems per plot (where present)					
$\bar{x}$	2.6	19.4	1.2	2.1	6.7
$\pm SD$	$\pm 4.3$	$\pm 17.6$	$\pm 0.9$	$\pm 2.0$	$\pm 5.1$
n	120	223	6	4	55
Range	1-35	1-108	1-3	1-7	1-27
Presence (% of plots)	53	99	3	2	25
Stems per ha (calculated)	298	3835	5	12	364
% of total	6.7	85.1	present	present	8.1
					100





Table 4. Stem diameters (dbh) for species of plants in the overstory of the lodgepole pine forest (based on 225 random samples).

Diameter class cm	Number of stems for each diameter class			
	White spruce	Lodgepole pine	Balsam	Aspen Willow
>18	1(+) <sup>a</sup>	4(+)		
>16-18		9(+)		
>14-16		59(1)		
>12-14	1(+)	69(1)		
>10-12	1(+)	306(7)		
>8-10	2(+)	709(16)		
>6-8	10(3)	843(20)		4(31) 2(+)
>4-6	26(8)	834(20)		11(2)
>2-4	120(38)	845(20)	1(17)	70(18)
>0-2	174(52)	637(15)	5(83)	326(80)
All classes	335(100)	4315(100)	6(100)	409(100)

<sup>a</sup>Number of stems; in brackets, percent that class is of the total stems for that species; (+) = present.



less in diameter.

Canopy height of the overstory varied from none to 11 m, with a mean of 7.3 and a standard deviation of  $\pm 2.1$  m. The slope of the forest floor on the random plots ranged from 1 to 33 degrees, with a mean of 9.2 and a standard deviation of  $\pm 5.1$  degrees.

Middlestory cover (Table 5, original data presented in Appendix 1) for all species combined occurred on 92 percent of the random plots, the most important cover values being: one, at 50 percent; and two, at 28 percent. Willow was present on 64 percent of the plots, usually at a cover value of one, while white spruce occurred on 42 percent of the plots, usually at a cover value of one. Alder was present on 45 percent of the plots, important cover values being: one, at 25 percent; and two, at 14 percent. Other species: lodgepole pine, rose (Rosa sp.), Canadian buffalo berry (Shepherdia canadensis), aspen, shrubby cinquefoil (Potentilla fruticosa), balsam poplar, and dwarf birch (Betula glandulosa) were present in lesser amounts.

Understory increased from very little in spring to almost complete cover in late summer. In both May and September, snow cover was often present. The melting snow in spring exposed twinflower (Linnaea borealis), pussy-toes (Antennaria sp.), bunchberry (Cornus canadensis),



Table 5. Frequency of distribution of cover values for the species of plants in the middlestory of the lodgepole pine forest (based on 225 random samples).

Cover <sup>a</sup> value	Species							
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil
								Rose
								Buffalo
								Total for all species combined
4						1		3
3	0.5 <sup>b</sup>				1	4		11
2	2.5	1	0.5	1	7	14	1	0.5
1	39	14	2.5	6	56	25	0.5	1
0	58	85	97	93	36	55	98	96.5
								85
								92
								8

<sup>a</sup>Cover values: 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.



bearberry (Arctostaphylos uva-ursi), wintergreen (Pyrola sp.) and all trees and shrubs too short to be counted as middlestory. Common blueberry (Vaccinium caespitosum) was found at lower elevations, while grouse-berry (Vaccinium scoparium) was found a little higher. Heart-leaved arnica (Arnica cordifolia), strawberry (Fragaria virginiana), northern bedstraw (Galium boreale), wild sweet pea (Lathyrus ochroleucus), wild vetch (Vicia americana), and hedysarum (Hedysarum spp.) appeared as the summer began. The dominant grass was pine grass (Calamagrostis rubescens). Asters (Aster spp.), senecios (Senecio spp.), fireweed (Epilobium angustifolium) and Indian paintbrush (Castilleja miniata) appeared as well.

Figures 4 to 11 show the variability present in lodgepole pine forest.

### Mixed forest

Overstory cover in the mixed forest (Table 6, original data in Appendix 2) was present on 98 percent of the plots, the most important cover values being: two, at 41 percent; and three, at 43 percent. There was no single dominant species, although white spruce cover was most common while willow was least common.

Stem density (Table 7) also shows no dominant species. Note the ubiquity of the white spruce in

Figure 4. Lodgepole pine forest showing: overstory cover -- lodgepole pine 5, total for all species combined 5; middlestory cover -- lodgepole pine 1, total for all species combined 1. The staff shows divisions of 0.25 m.

Figure 5. Lodgepole pine forest showing: overstory cover -- lodgepole pine 5, total for all species combined 5; middlestory cover -- total for all species combined 0. The staff shows divisions of 0.25 m.



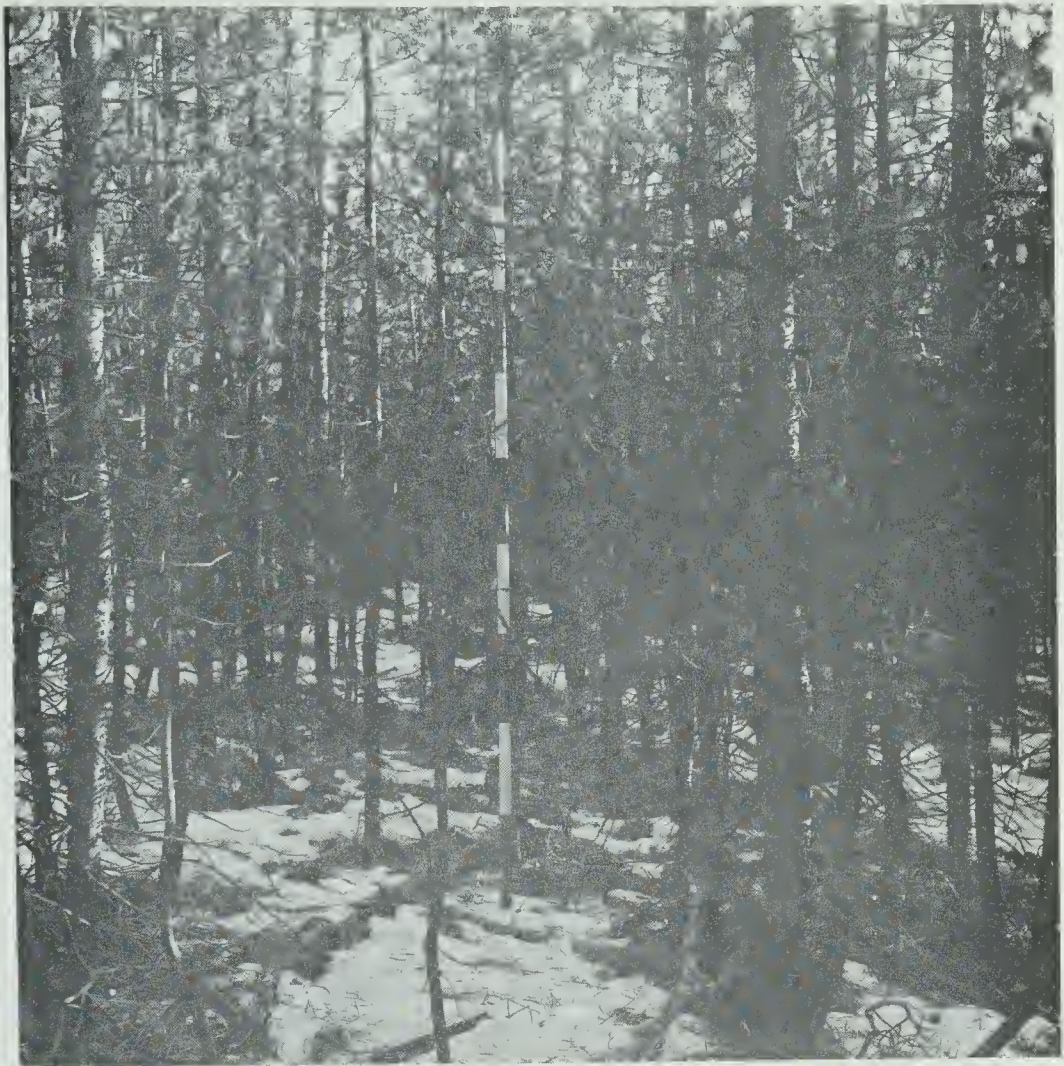




Figure 6. Lodgepole pine forest showing: overstory cover -- lodgepole pine 4, total for all species combined 4; middlestory cover -- alder 3, willow 1, total for all species combined 3. The staff shows divisions of 0.25 m.

Figure 7. Lodgepole pine forest showing: overstory cover -- lodgepole pine 3, total for all species combined 3; middlestory cover -- willow 1, total for all species combined 1. The staff shows divisions of 0.25 m.

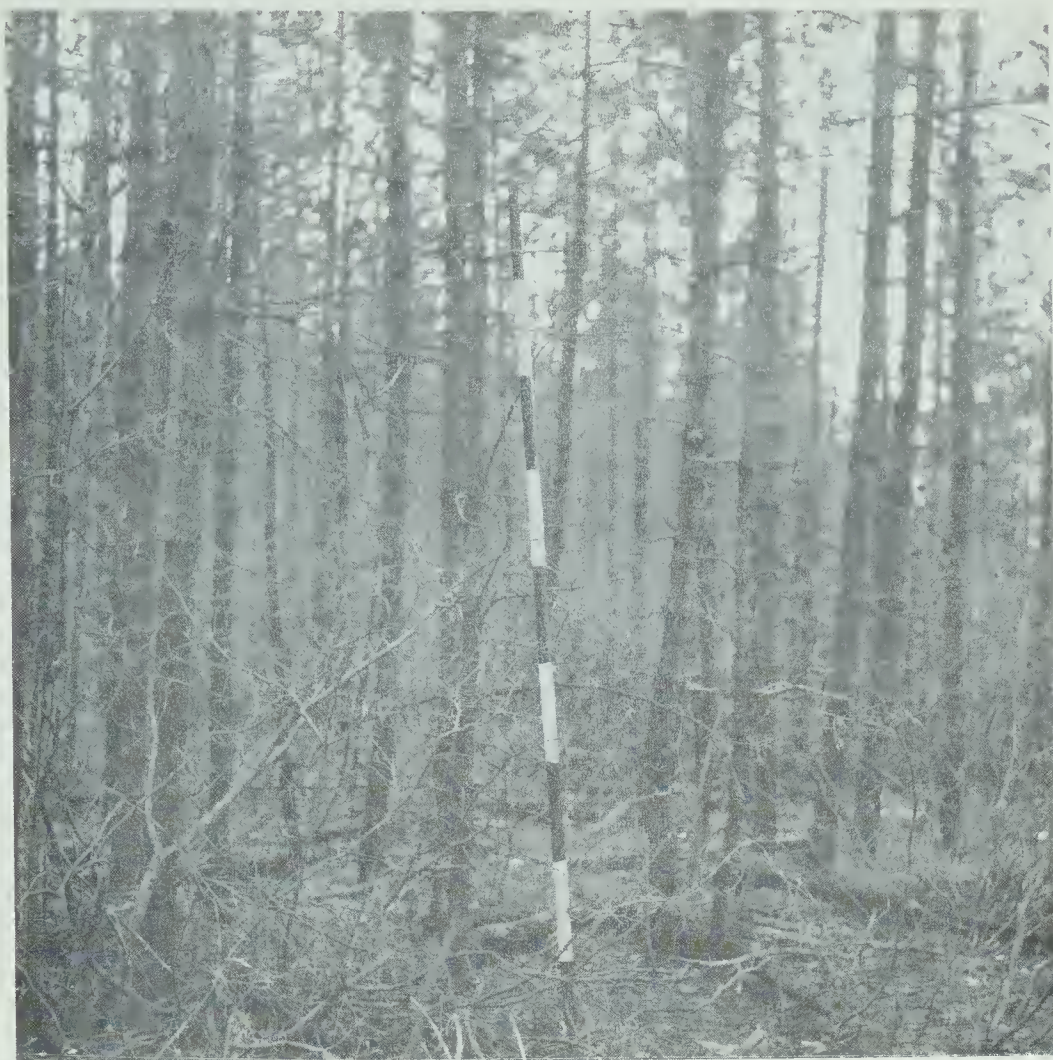


Figure 8. Lodgepole pine forest showing: overstory cover -- lodgepole pine 2, white spruce 2, willow 2, total for all species combined 3; middlestory cover -- willow 1, total for all species combined 1. The staff shows divisions of 0.25 m.

Figure 9. Lodgepole pine forest showing: overstory cover -- lodgepole pine 2, total for all species combined 2; middlestory cover -- alder 3, willow 1, total for all species combined 3. The staff shows divisions of 0.25 m.



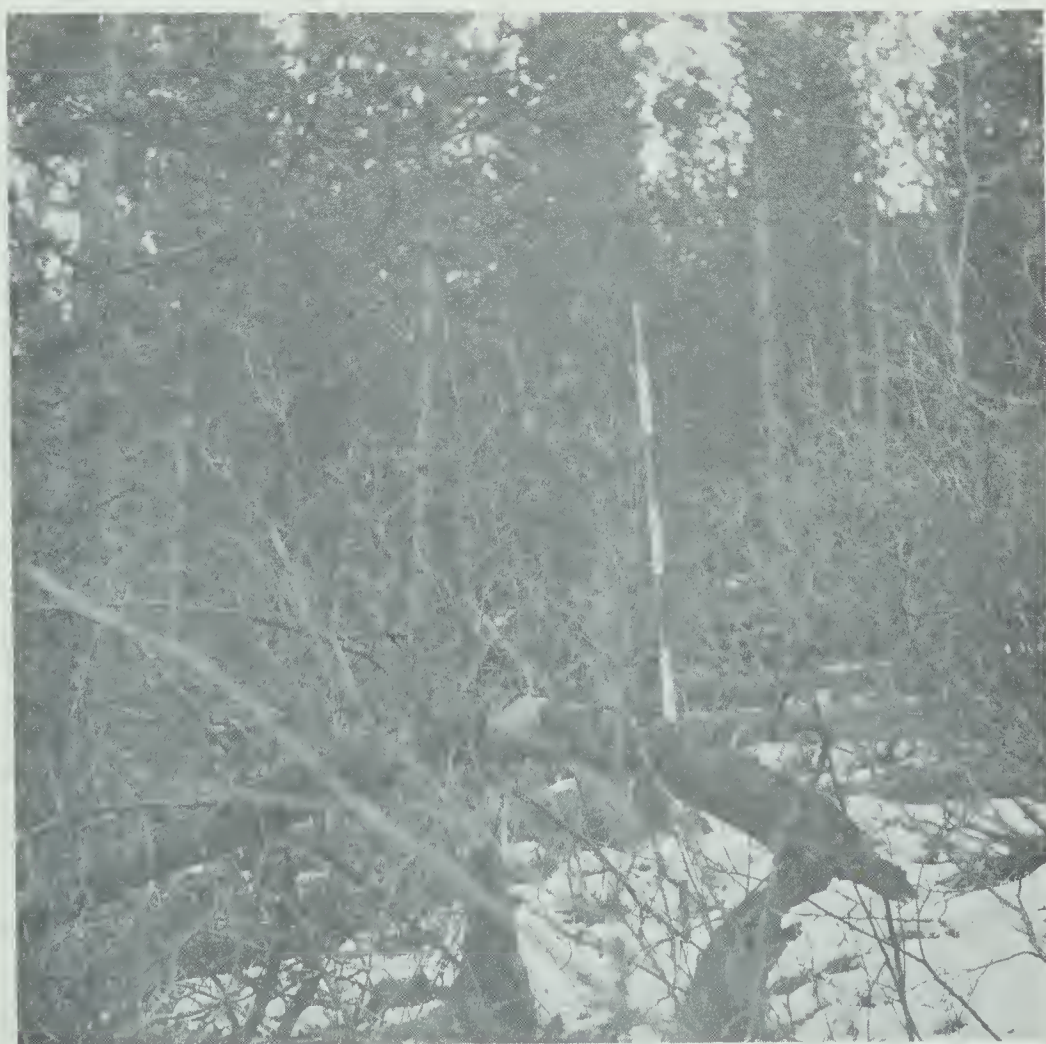


Figure 10. Lodgepole pine forest showing: overstory cover -- lodgepole pine 2, total for all species combined 2; middlestory cover -- willow 1, total for all species combined 1. The staff shows divisions of 0.25 m.

Figure 11. Lodgepole pine forest showing: overstory cover -- lodgepole pine 2, total for all species combined 2; middlestory cover -- lodgepole pine 1, total for all species combined 1. The staff shows divisions of 0.25 m.



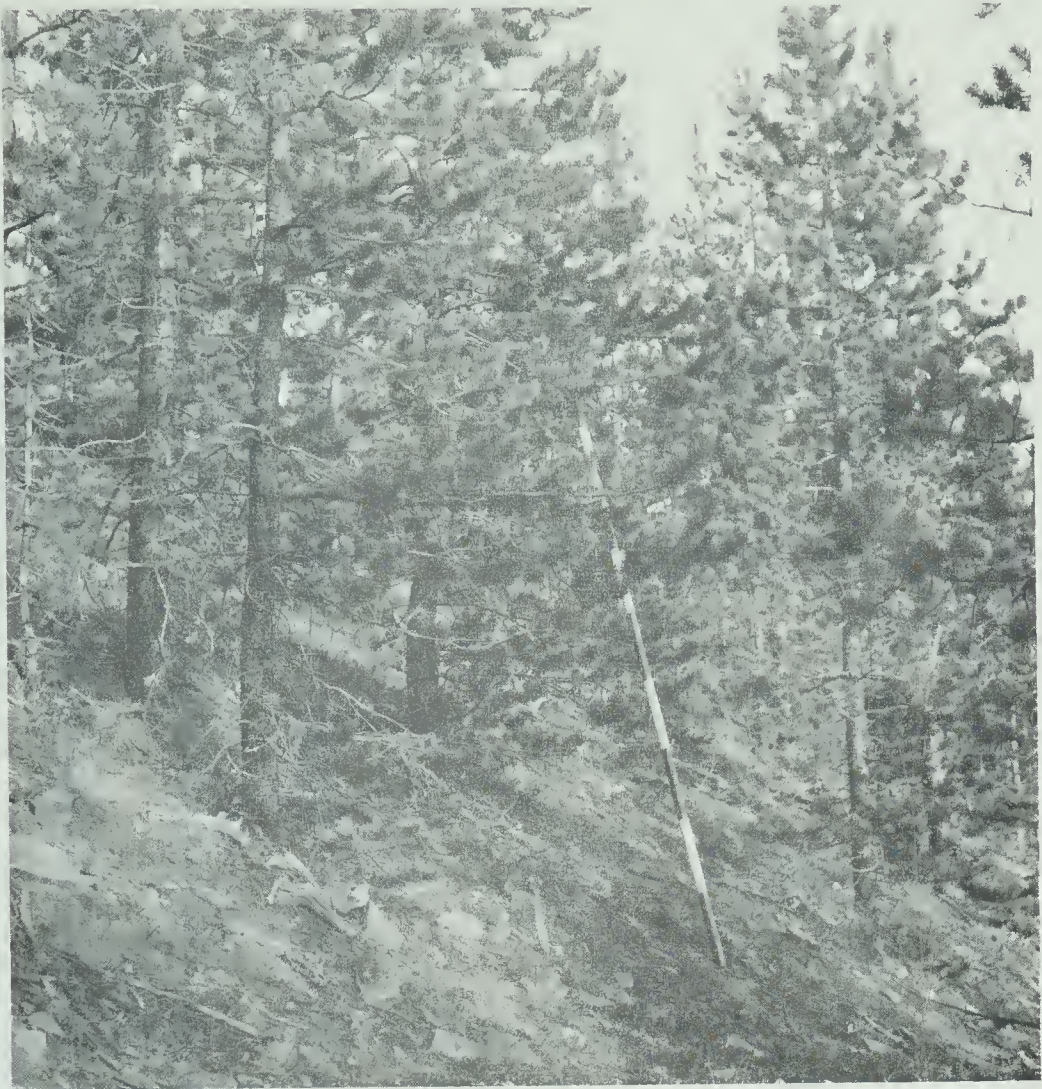






Table 6. Frequency distribution of cover values for species of plants in the overstory of the mixed forest (based on 46 random samples).

Cover value <sup>a</sup>	Species					Total for all species combined
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow	
5						2 <sup>b</sup>
4		2		2		4
3	2 <sup>b</sup>	2	6	9	2	43
2	39	45	28	30	9	41
1	39	11	13	11	17	7
0	20	39	53	48	72	2

<sup>a</sup>Cover values: 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.



Table 7. Stem density for species of plants in the overstory of the mixed forest (based on 46 random samples).

Density	Species				
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow
					All species combined
Stems per plot (where present)					
$\bar{x}$	3.2	5.9	9.1	7.8	7.1
$\pm$ SD	$\pm 3.0$	$\pm 7.4$	$\pm 3.2$	$\pm 6.9$	$\pm 7.3$
n	37	28	22	24	13
Range	1-12	2-42	2-20	3-26	3-28
Presence (% of plots)	80	61	47	52	28
Stems per ha(calculated)	509	626	876	817	400
% of total	15.7	12.4	27.2	25.3	12.4



comparison to other species, which are more clumped. Lodgepole pine and white spruce were present at 626 and 509 stems per ha respectively, while balsam poplar and aspen were present in densities of 876 and 817 stems per ha respectively. Willow occurred at 400 stems per ha. The stem density of all species combined was 3230 per ha.

Stem diameters (dbh) for the overstory (Table 8) were larger for lodgepole pine and the two poplars, while white spruce was largely composed of smaller trees. This would be expected as a white spruce climax begins to replace the mixed forest.

Canopy height of the overstory varied from none to 12 m, with a mean of 6.9 and a standard deviation of  $\pm 2.1$  m. The slope of the forest floor on the random plots ranged from 0 to 28 degrees, with a mean of 6.5 and a standard deviation of  $\pm 5.3$  degrees.

Middlestory cover (Table 9, original data presented in Appendix 2) was present in 96 percent of the random plots, the most common cover values being: one, at 27 percent; and two, at 58 percent. Willow and white spruce were present on 72 and 63 percent of the plots respectively; other species were present to a lesser extent.

Species present in the understory of the lodgepole



Table 8. Stem diameters (dbh) for species of plants in the overstory of the mixed forest (based on 46 random samples).

Diameter class cm	Number of trees for each diameter class			
	White spruce	Lodgepole pine	Balsam poplar	Aspen  Willow
>16-18		1(1)		
>14-16		3(2)		
>12-14		9(8)		2(1)
>10-12		19(13)	1(+)	7(49)
>8-10	2(2) <sup>a</sup>	19(13)	11(5)	24(13)
>6-8	7(6)	26(19)	25(13)	17(19)
>4-6	15(13)	13(9)	25(13)	44(23) 3(3)
>2-4	45(38)	28(19)	57(28)	50(27) 9(10)
>0-2	48(41)	26(18)	83(41)	44(33) 80(87)
All classes	117(100)	144(100)	202(100)	188(100) 92(100)

<sup>a</sup>Number of stems; in brackets the percent that class is of the total stems for that species; (+) = present.





Table 9. Frequency distribution of cover values for species of plants in the middlestory of the mixed forest (based on 46 random samples).

Cover <sup>a</sup> value	Species									
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo Total for all species combined
3		4			4	9				11
2	7 <sup>b</sup>		4		33	15			7	58
1	56	16	23	26	37		4	7	11	27
0	37	80	71	74	28	76	96	93	89	4

<sup>a</sup>Cover values: 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.



pine forest were also present in the understory of the mixed forest. I also found wheat grass (Agropyron sp.), goldenrod (Solidago sp.), dandelion (Taraxacum officinale), yarrow (Achillea millefolium), violet (Viola sp.) and lousewort (Pedicularis sp.).

Mixed forest was variable and ranged from pure aspen stands, with or without white spruce, through mixed forest of all species to isolated patches of lodgepole pine (Figs. 12 to 14).

#### White spruce forest

Overstory cover (Table 10, original data in Appendix 3) for all species combined occurred in 100 percent of the plots, the most important cover values being: two, at 29 percent; three, at 41 percent; and four, at 24 percent. White spruce was dominant, the most important cover values being: two, at 24 percent; and three, at 47 percent. Other species contributed little to the overstory cover.

Stem density (Table 11) was greatest for white spruce, which, where present, averaged 9.1 stems per plot, an average of 1706 stems per ha. Other species were present in much lower densities. The average for all species combined was 2153 stems per ha.

Stem diameters (dbh) for the overstory (Table 12) were greatest for white spruce. Sixty-eight percent of

Figure 12. Mixed forest showing: overstory cover -- aspen 4, total for all species combined 4; middlestory cover -- total for all species combined 0. The staff shows divisions of 0.25 m.

Figure 13. Mixed forest showing: overstory cover -- white spruce 3, aspen 2, total for all species combined 3; middlestory cover -- balsom poplar 1, white spruce 1, willow 1, total for all species combined 2. The staff shows divisions of 0.25 m.





Figure 14. Mixed forest showing: overstory cover -- willow 2, total for all species combined 2; middlestory cover -- alder 2, willow 2, lodgepole pine 1, total for all species combined 3. The staff shows divisions of 0.25 m.

Figure 15. White spruce forest showing: overstory cover -- white spruce 3, total for all species combined 3; middlestory cover -- willow 2, white spruce 1, total for all species combined 2. The staff shows divisions of 0.25 m.









Table 10. Frequency distribution of cover values for species of plants in the overstory of the white spruce forest (based on 17 random samples).

Cover value <sup>a</sup>	Species				
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow
5	6 <sup>b</sup>				6
4	17				24
3	47				41
2	24				29
1		6	6	6	24
0	6	94	94	94	76

<sup>a</sup>Cover values: 5=>75=95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.



Table 11. Stem density for species of plants in the overstory of the white spruce forest (based on 17 random samples).

Density	Species				
	White spruce	Lodgepole pine	Balsam poplar	Aspen	Willow
Total for all species combined					
Stems per plot (where present)					
$\bar{x}$	9.1	2	4	2	7.5
$\pm$ SD	<u>4.7</u>				<u>5.1</u>
n	16	1	1	1	4
Range	2-22				3-12
Presence (% of plots)	94	6	6	6	24
Stems per ha (calculated)	1706	24	47	24	353
% of total	79.3	1.1	2.1	1.1	16.4
					100



Table 12. Stem diameters (dbh) for species of plants in the overstory of the white spruce forest (based on 17 random samples).

Diameter class cm	Number of trees for each diameter class			
	White spruce	Lodgepole pine	Balsam poplar	Aspen Willow
>25-30	12(8) <sup>a</sup>			
>20-25	12(8)			
>18-20	8(6)			
>16-18	4(3)			
>14-16				
>12-14	13(9)			
>10-12	9(6)			
>8-10	14(10)			
>6- 8	12(8)			
>4- 6	15(10)	1(50)		
>2- 4	33(23)	1(50)	2(50)	4(13)
>0- 2	13(9)		2(50)	26(87)
Total all species	145(100)	2(100)	4(100)	30(100)

<sup>a</sup>Number of stems; in brackets the percent that each class is of the total stems for that species.



the white spruce stems were greater than four cm in diameter, while nearly all the stems of the other species were four cm or less in diameter.

Canopy height of the overstory varied from 4 to 20 m, with a mean of 13.9 and a standard deviation of  $\pm 3.7$  m. The slope of the forest floor on the random plots ranged from 1 to 10 degrees, with a mean of 3.8 and a standard deviation of  $\pm 2.9$  degrees.

Middlestory cover (Table 13, original data presented in Appendix 3) for all species combined occurred on 88 percent of the random plots, the most important cover values being: one, at 53 percent; and two, at 35 percent. Willow was present on 65 percent of the plots, while other species were present to a lesser degree.

Rush, horsetail (Equisetum sp.) and sedges (Carex spp.) were present in the understory. As well, common blueberry, twinflower, bunchberry, wintergreen and orchids (Habenaria spp.) were found.

Figure 15 shows typical white spruce forest.

#### Meadow and marsh

Overstory, although occasionally present in this vegetation type, was not described, as none fell into a random plot. The slopes of the random plots ranged from 0 to 10 degrees, with a mean of 4.0 and a standard





Table 13. Frequency distribution of cover values for species of plants in the middlestory of the white spruce forest (based on 17 random samples).

Cover value <sup>a</sup>	Species							
	White spruce	Lodge- pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinque- foil
2					30			
1	29 <sup>b</sup>		6	12	35		17	6
0	71	100	94	88	35	100	100	83
								17
								83
								94
								83
								12
								35
								53
								12
								36

<sup>a</sup>Cover values: 2=>5-25%, 1=present-5%, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.



deviation of  $\pm 3.1$  degrees.

Middlestory cover (Table 14, original data presented in Appendix 4) was present in 68 percent of the plots, the most important cover values being: two, at 32 percent, and three, at 26 percent. Willow was present on the largest number of plots, while other species were present in lesser amounts. Figures 16 and 17 show typical meadow and marsh.



Table 14. Frequency distribution of cover values for species of plants in the middlestory of meadow and marsh (based on 22 random samples).

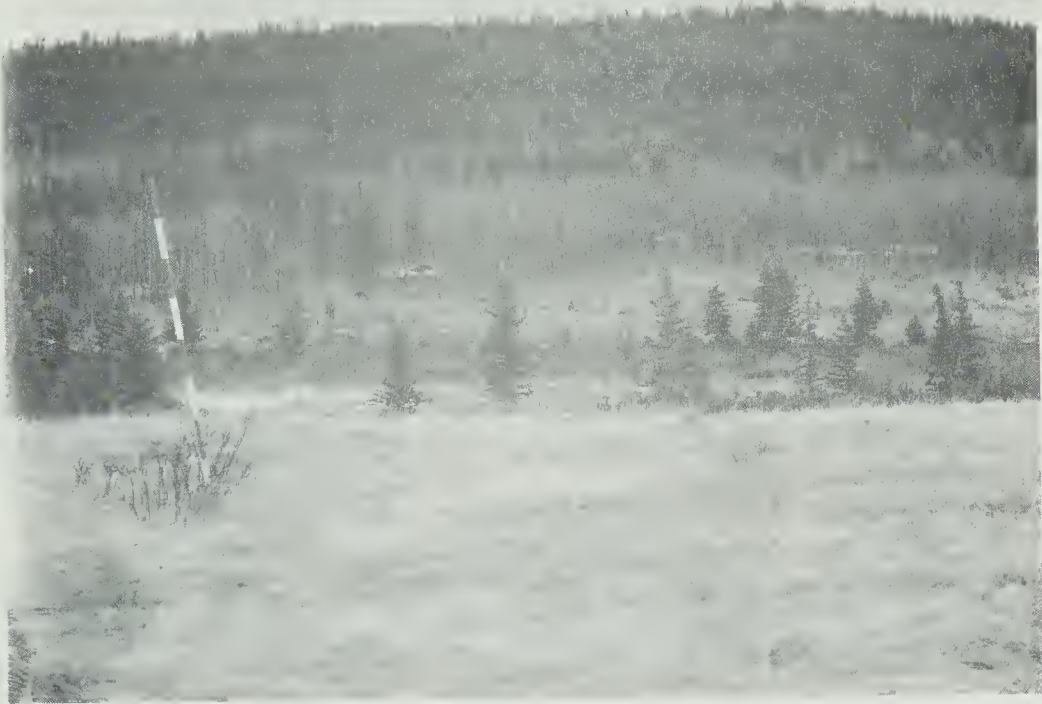
Cover value <sup>a</sup>	Species							
	White spruce	Lodge- pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinque- foil
							Rose berry	Buffalo Total for all species combined
4					5			5
3					18			26
2					32		5	32
1	9 <sup>b</sup>			9	9	5	9	5
0	91	100	100	91	36	95	86	32

<sup>a</sup>Cover values: 4=>50-95%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.

<sup>b</sup>Percent of each cover value for each species and for all species combined.

Figure 16. Meadow and marsh showing: overstory cover -- absent; middlestory cover -- willow 1, total for all species combined 1. The staff shows divisions of 0.25 m.

Figure 17. Meadow and marsh showing: overstory cover -- absent; middlestory cover -- willow 3, total for all species combined 3. The staff shows divisions of 0.25 m.







## SEX AND AGE DETERMINATION

Sex determination

No difficulties were encountered in sex determination of Franklin's grouse by plumage characteristics, using the methods outlined by Lumsden and Weeden (1964), Stoneberg (1967), Zwickel and Martinsen (1967), and Ellison (1968b).

Age determination

The primary requirement of any age determination technique is precision, most acute in small populations where an improperly classified bird could appreciably affect the age ratios.

I found age determination by outer primaries (Petrides, 1942; Stoneberg, 1967, Zwickel and Martinsen, 1967; and Ellison, 1968b), and by tails (Zwickel and Martinsen, 1967) were, with respect to the precision required, unsatisfactory for field studies on live birds, as birds could only be examined for a few minutes and could not be taken for comparison with others. Stoneberg (1967) noted that the length of the central rectrices could be used in age determination. I expanded Stoneberg's method and took three feathers: a first primary, a central upper tail covert, and a central rectrix. The idea here is that the post-juvenal



feathers, grown while the birds are juveniles and only a fraction of their future adult weights, would be smaller.

I considered four age groups: juveniles, yearlings, young adults and older adults. Males were considered juveniles while in the brood, and became yearlings in their first fall after dissolution of the broods. Yearlings, although superficially similar to adults, could be distinguished from adults by the three requisite feathers. Yearlings became adults at the end of their second summer, and older adults at the end of their third. Unless banded previously as yearlings, the ages of males in the two classes of adults were indistinguishable.

The first primary, the most proximal, is lost in early June and replaced again by mid-August, while central rectrices and upper tail coverts are lost in late June, and renewed by early September. The measurements of the widths at the superior umbilicus (to the nearest 0.1 mm), were plotted against the lengths (to the nearest mm), for all first primaries (Fig. 18), central rectrices (Fig. 19) and central upper tail coverts (Fig. 20) collected. Note that in each figure the points are grouped into two clusters. When only feathers from males whose ages were known from the year of banding are considered, the factor which separates the two clusters is the age of

Figure 18. Scatter diagram for first primaries  
from male Franklin's grouse of known  
and assigned age.

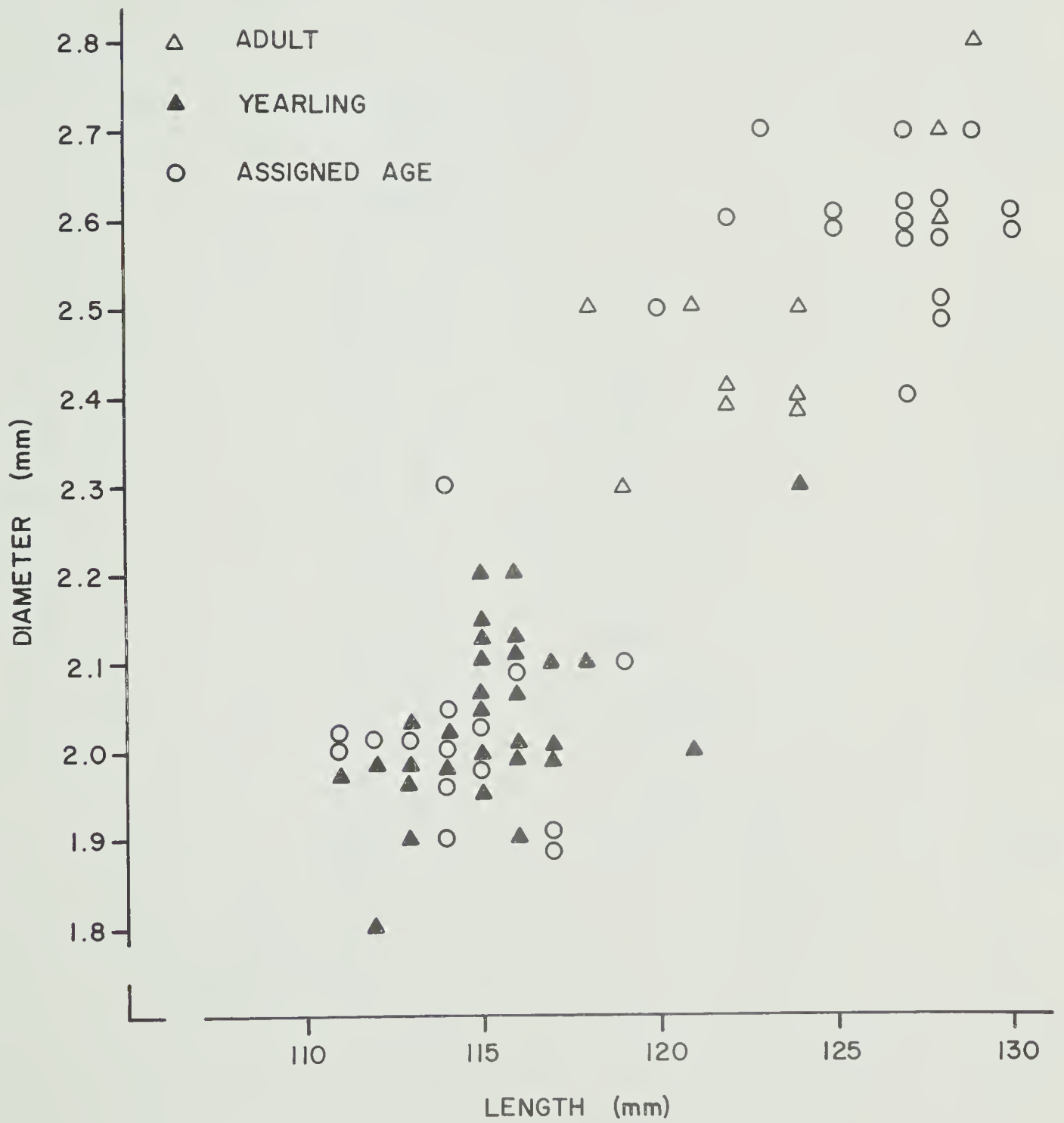


Figure 19. Scatter diagram for central rectrices from male Franklin's grouse of known and unknown age.

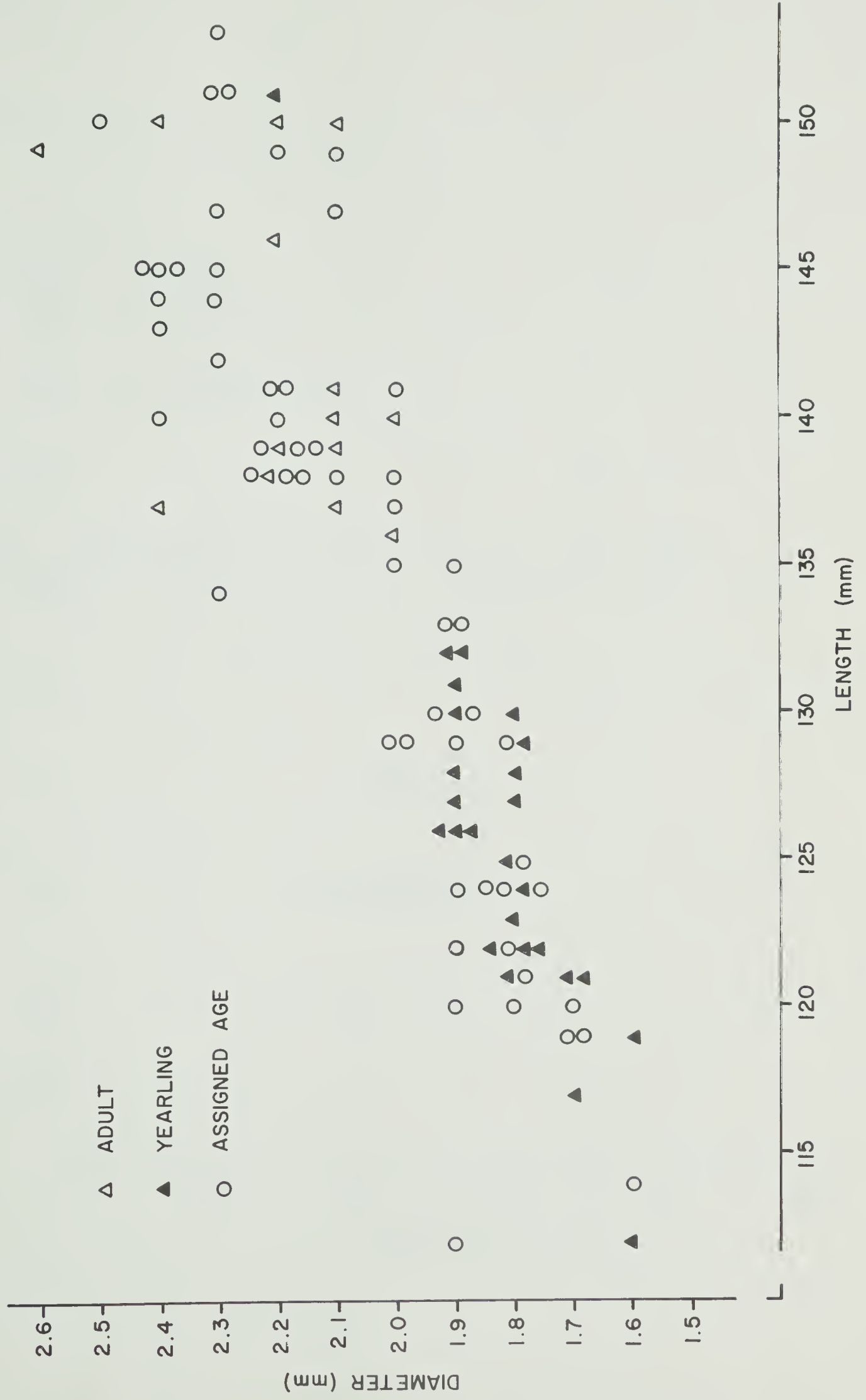
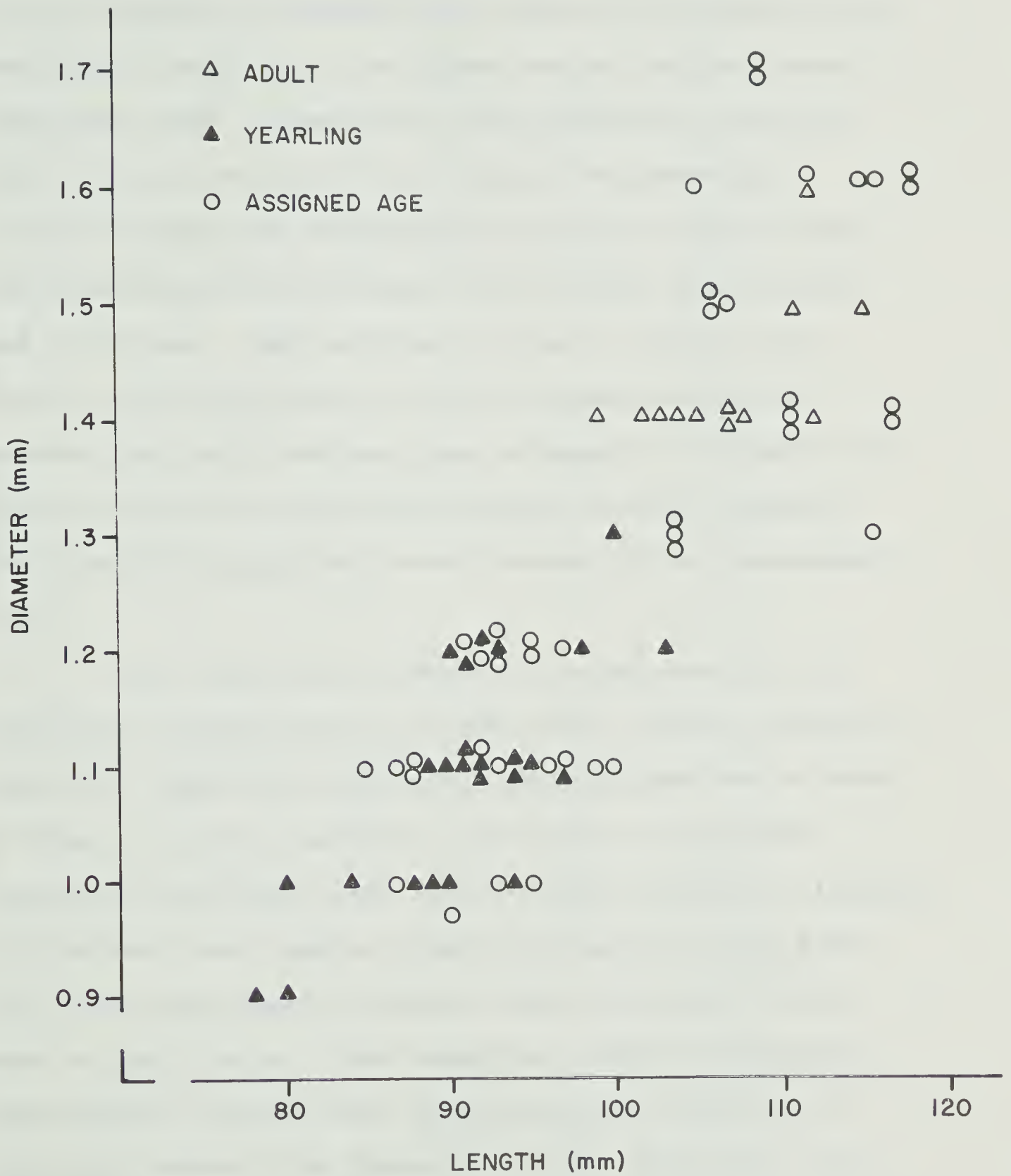


Figure 20. Scatter diagram for central upper tail  
coverts from male Franklin's grouse of  
known and assigned age.







the males from which the feathers were taken.

I chose discrimination functions which appeared totally mutually exclusive for feathers from adults and yearlings (Table 15). To assure mutual exclusiveness, I purposely chose conservative discrimination functions. Table 15 also shows the size ranges for uncertain feathers found, the measurements of which fell between the discrimination functions for feathers from adults and yearlings. The uncertain category itself would include the measurements of all feathers which fell between the adult and yearling categories. No male was found to have more than one feather in this category. These uncertain feathers were ignored in age determination.

Most males were banded in spring when all the requisite feathers were available, but others, banded in the early summer during moult, often lacked one or more of them. No male, however, was found to have both naturally occurring adult and yearling feathers, although if feathers were removed from yearlings in their first fall, the replacement feathers found the next spring were of adult size. This would be expected, as these replacement feathers were grown when the bird was of yearling, rather than juvenile, size. Males were thus assigned an age if any feather or feathers fell in the



Table 15. Discrimination functions for the three feathers used in assessing the age of male Franklin's grouse. All measurements are in mm.

Age of grouse	First primary		Central rectrix		Upper tail covert	
	Diam.	Length	Diam.	Length	Diam.	Length
Adult	$\geq 2.4$ and $\geq 118$		$\geq 2.1$ and $\geq 136$		$\geq 1.4$ and $\geq 100$	
Uncertain <sup>1</sup>	2.3 and 114-124		2.0 and 134-135		1.3 and 100-115	
Yearling	$\leq 2.2$ and $\leq 117$		$\leq 1.9$ and $\leq 133$		$\leq 1.2$ and $\leq 104$	

<sup>1</sup>Measurements of feathers found; the true discrimination functions of the uncertain categories would include all measurements of feathers which did not fall within the discrimination functions for adults or yearlings.



yearling or adult category. Of 43 unbanded males which yielded feathers, only one remained of unknown age. But a central rectrix falling into the uncertain category was available for this bird; had other feathers been available, this bird's age would probably have been resolved.

Males banded during later summer when all requisite feathers were moulted were indistinguishable as to age and were of "unknown age".

To summarize, this method of age determination will distinguish yearlings from adults from September to mid-June, but is inoperative in midsummer during the moult. Due to possible geographic variation, I would not recommend direct application of these discrimination functions to other populations of Franklin's grouse without testing, while their application to other subspecies of spruce grouse would require even more caution.

Weights were also examined as a possible method of age determination. Males from all years of the study were pooled (Fig. 21). A comparison of the weights of 33 adults and 31 yearlings from 1 May to 31 August showed that adults were heavier (Table 16). The difference was significant [ $P, 60 \text{ df}, (t \geq 3.55) < 0.05$ ]. Most weights, however, were recorded in spring.

As adult males appeared sexually active in May



Figure 21. Recorded weights of adult and yearling male Franklin's grouse from 1 May to 31 August, 1965 to 1968.

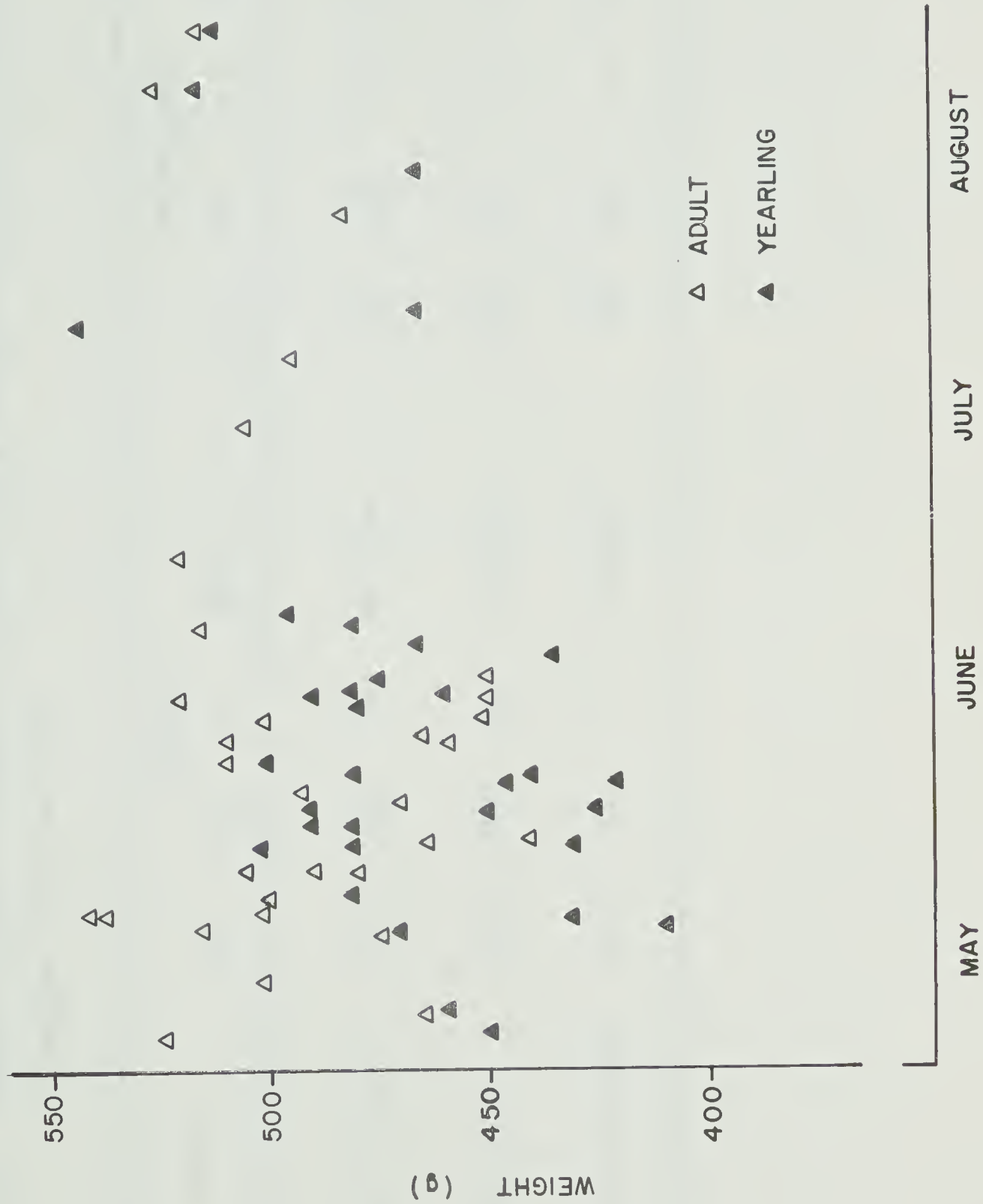




Table 16. Weights of male Franklin's grouse in g during the period 1 May to 31 August, 1965 to 1968.

Time period	Adults			Yearlings				
	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
1 May-31 August	494	$\bar{+26}$	33	440-540	469	$\bar{+30}$	31	420-540
1 May-15 June	490	$\bar{+27}$	25	440-540	462	$\bar{+26}$	22	420-520
16 June-31 August	505	$\bar{+18}$	8	495-525	486	$\bar{+33}$	9	465-540



and early June, I assigned limits to the breeding period of 1 May to 15 June. During this period adults were heavier than yearlings (Table 16). The difference was significant [ $P, 46 \text{ df}, (23.57) < 0.05$ ]. A comparison of yearling and adult weights after the breeding period (Table 16) showed no significant difference. The sample size, however, was very small, although it seems reasonable to expect yearling weights to approach those of adults as yearlings near adult age.

These results show that adults are heavier than yearlings in spring, but that since yearling and adult weights overlap, age determination by weight alone is unsatisfactory.





PATTERNS OF DISPERSION IN MALE FRANKLIN'S GROUSE

THE POPULATION

Fifty-three yearling and adult males were found on the main study area during the course of the study, while 19 were found on the auxiliary study area (Table 17). In 1965 and 1966 new adults were found during expansion of the main study area. Otherwise the majority of new birds found in the population were yearlings (yearlings previously banded as juveniles included) while new adults were few (adults previously banded as yearlings not included). The two new adults found in 1967 had originally been banded as adults on the auxiliary study area, while the new adult in 1968 was probably a newcomer. I believe all adults on the main study area were found in 1967 and 1968. Yearling males, more difficult to find, were probably not all found, although I believe the unfound birds were few.

The age composition of the population of the main study area (Table 18) could only be compared for 1967 and 1968 because of the presence of males of unknown age in earlier years. A chi-square test showed no significant difference in age composition of the population for these two years. I believe the population size and structure was quite similar during the four years of the study.

The density of males on the main study area in 1967 and 1968 averaged 4.8 males per square km, of which



Table 17. New yearling and adult male Franklin's grouse recorded on the main and auxiliary study areas.

Year	Main study area			Auxiliary study area		
	Yearlings	Adults	Unknown age	Yearlings	Adults	Unknown age
1965	4	3	9	0	1	4
1966	7	6	2	0	4	3
1967	11	(2) <sup>a</sup>	0	1	6	0
1968	8	1	0	not searched		
All years	30	10(2)	11	1	11	7
Total males		51(2)			19	

<sup>a</sup>Originally banded as adults in 1966 on the auxiliary study area.



Table 18. Age composition of the population of male Franklin's grouse on the main study area for the years 1965 through 1968.

Age	1965	1966	1967	1968
Adults	4	13	18	19
Percent of total	21%	57%	62%	68%
Yearlings	4	7	11	9
Percent of total	21%	30%	38%	32%
Unknown age	11	3	0	0
Percent of total	58%	13%	0	0
Total - all ages	19	23	29	28

3.1 were adults and 1.7 were yearlings. Stoneberg (1967), on a study area of about 2.5 square km in Montana, had an average population in 1965 and 1966 of 2.9 males per square km, of which 2.3 were adults and 0.6 were yearlings. Ellison (1968a), on a study area of about 5.1 square km in Alaska, had an average population of 3.9 males per square km in 1965 and 1966 and 2.7 males in 1967, of which 30 percent were adults and 70 percent



were yearlings. The density of Franklin's grouse in this study was higher than in the populations in Montana or Alaska. I found the ratio of adults to yearlings to be higher than in the Alaska population, but lower than in the Montana population.

PATTERNS OF DISPERSION AS A FUNCTION OF THE AGE OF MALE  
FRANKLIN'S GROUSE

Stoneberg (1967) in Franklin's grouse and Ellison (1968a) in Alaska spruce grouse reported differences in the dispersion of adults and yearlings. These differences are not unique to spruce grouse as Boag (1965) and Bendell and Elliott (1966) in blue grouse (Dendragapus obscurus), Choate (1963) in white-tailed ptarmigan (Lagopus leucurus), and Marshall (1965) and Gullion (1967) in ruffed grouse (Bonasa umbellus) found differences in dispersion of adults and yearlings.

Movements of males over the spring and summer

Spring and summer movement was grouped into four types: "no large movement"; "large movement and return"; "large movement and no return"; and "observed once and not observed again". Males showing "no large movement" appear localized over the spring and summer. Examples are shown in Figure 22 (males 5, 6, 10 etc.) and Figure 23



Figure 22. Locations of observations of male Franklin's grouse  
on the main study area 1 May to 15 September 1966.  
Individual males are numbered.

0 500 m

--- STREAM

— STUDY AREA BOUNDARY

→ MOVEMENT AND DIRECTION

ADULT ○ △ □ ○

YEARLING ● ▲ ■ ●

UNKNOWN AGE ▣ ▲

1966

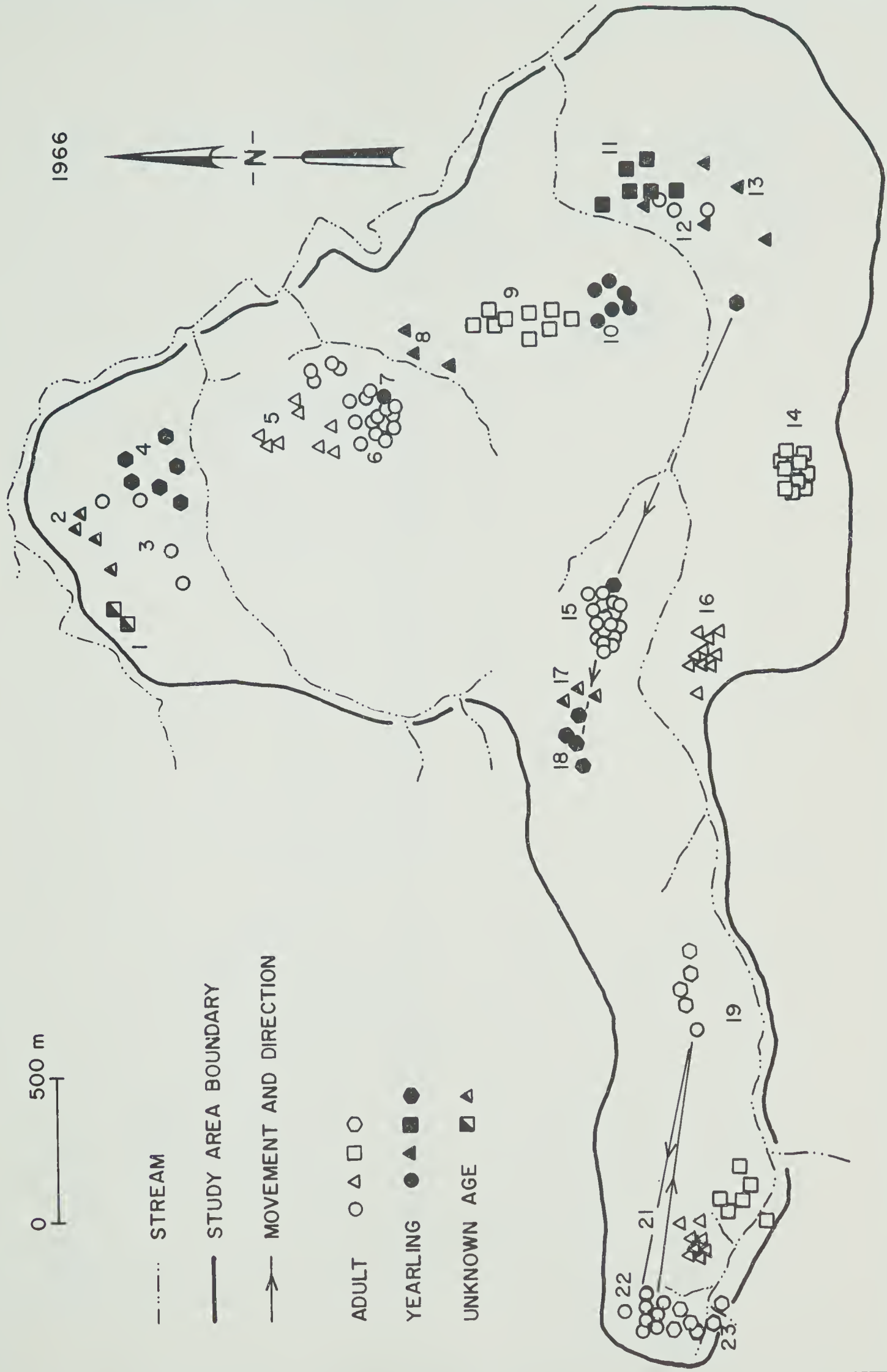
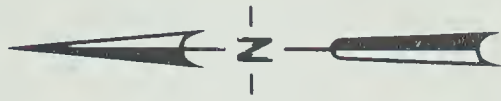


Figure 23. Locations of observations of male Franklin's grouse on the main study area 1 May to 15 September 1967. Individual males are numbered.

0 500 m

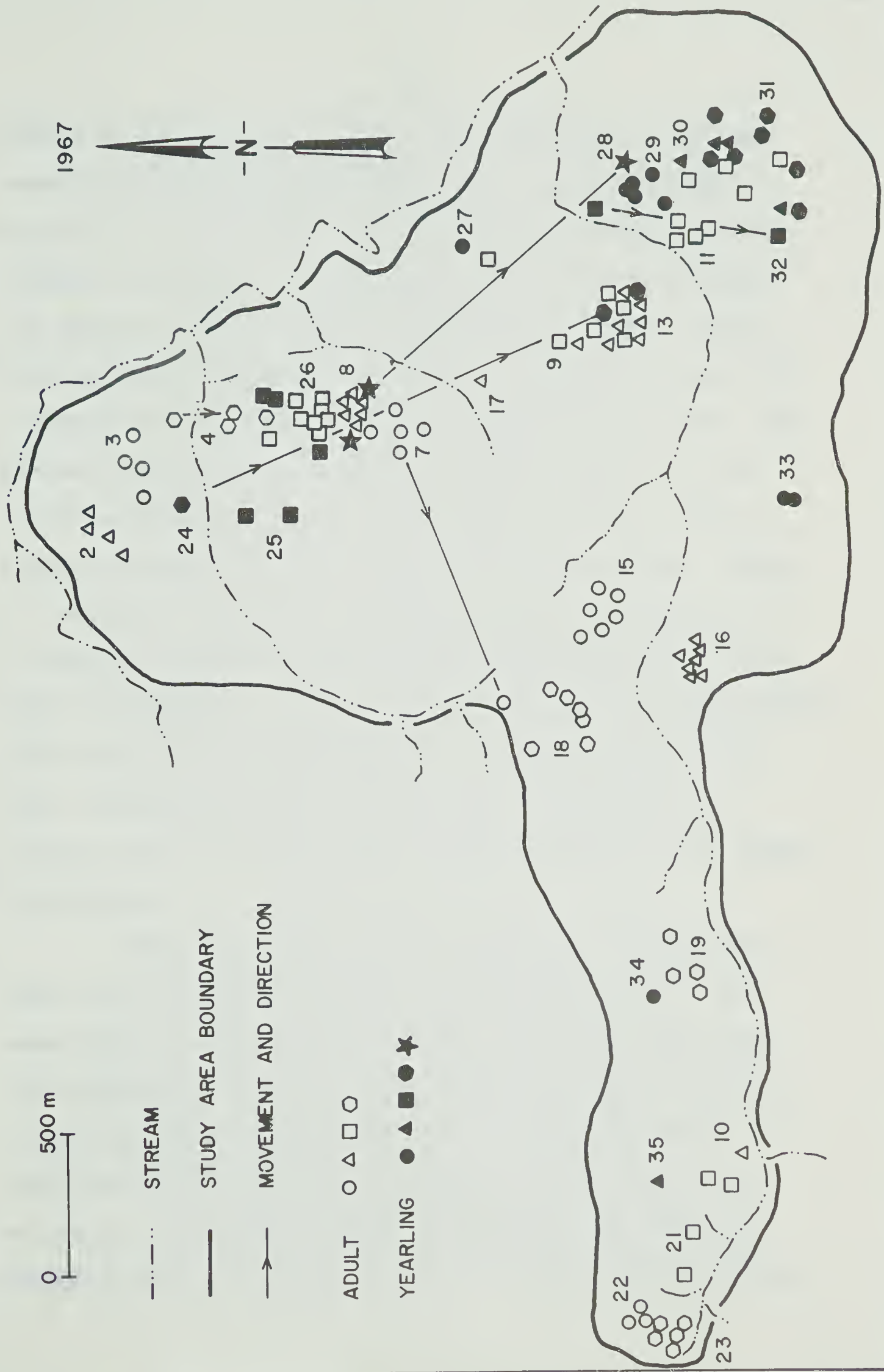
--- STREAM

— STUDY AREA BOUNDARY

→ MOVEMENT AND DIRECTION

ADULT ○ △ □ ○

YEARLING ● ▲ ■ ● ★





(males 8, 15, 19 et.). Most adults and some yearlings showed this localization (Table 19). Large movement was said to occur when a male crossed a natural barrier (stream, opening in the forest or hill) or moved from the general area in which it was usually found. Males showing "large movement and return" (Figure 22, male 22) occurred for both adults and a yearling (Table 19). The distances moved by this group of males (Table 20) are probably minimal and, had the study area been larger, greater distances would probably have been found. Chase by predators, pursuit of another male, the following of a female or wandering are possible explanations of this type of movement. Ellison (1968a) found three males which would seem to fit this category. As males returned to their localized areas, I suggest this category is a special case of the preceding one, and that the two might be grouped.

Seven yearlings (Table 19) showed "large movement and no return" (Figure 23, male 24 and 28). As none showed localization to begin with, they were probably wandering. The distances moved (Table 20) by this group are again probably minimal. Stoneberg (1967) found two yearlings which seemed to show this type of movement. Two adults (Table 19) showed this type of movement (Fig. 23, males 4 and 7). Male seven may have





Table 19. Types of movements undertaken by male Franklin's grouse.

Type of movement	Age	
	Yearlings	Adults
"No large movement"	10	51
"Large movement and return"	1	4
"Large movement and no return"	7	2
"Observed once and not observed again"	11	1

moved away or have been killed, while male four may have been a case of "large movement and return". "Observed once and not observed again" was quite common for yearlings but was observed only once in adults (Fig. 23, males 17, 27, 34, etc.). These males may have moved away or have been killed. Stoneberg (1967) found several yearlings only once. Had yearlings been easier to find, I believe many would have been found to be wandering and would have fallen in the group showing "large movement and no return". Perhaps these two categories could be grouped.

If the males of the group which included "no large movement" and "large movement and return" were



Table 20. Distances moved by male Franklin's grouse over the summer for the males in the categories involving "large movement". All distances are shown in m.

Type of movement	Adults			Yearlings				
	$\bar{x}$	+SD	n	range	$\bar{x}$	+SD	n	range
Large movement and return	395	+375	4	360-1120	350	+156	2 <sup>1</sup>	240-460
Large movement and no return	740	+594	2	320-1160	1100	+582	7	280-1960

<sup>1</sup>An individual yearling which moved twice.



compared with males of the group which included "large movement and no return" and "observed once but not observed again", adults appeared significantly more localized than yearlings ( $\chi^2(1df) = 31.1^*$ ).

#### Locating and measuring home ranges

Animals, when restricted to definite areas, are said to occupy home ranges (Odum, 1959). Thus, males of the previous section, both yearlings and adults which fell in the categories "no large movement" and "large movement and return", occupied home ranges. I calculated the size and location of home ranges by mapping the sighting points of each male and measuring the maximum polygon formed by joining the outermost points. Home ranges can be estimated for the localized males in Figures 22 and 23.

#### Transportation experiments

Transportation experiments, while perhaps demonstrating differences in navigational ability, may also give an indication of the attachment of male Franklin's grouse for their home ranges. Gullion (1962) used transportation experiments to show the attachment of Gambel's quail (Lophortyx gambeli) to certain areas.

Of the five adults transported, all returned to their home ranges, but of the three yearlings transported,



two were never seen again and one was found the next spring near the release site (Table 21). These data suggest adults are more firmly attached to their home ranges than are yearlings.

Table 21. The homing of male Franklin's grouse to their home ranges.

Age	Date moved	Distance moved(m)	Results
Adult	28 May 1967	1400	Observed back 5 June 1967
Adult	4 June 1967	1900	Observed back 15 June 1967
Adult	21 July 1967	1300	Observed back 25 July 1967
Adult	21 August 1966	1200	Observed back 26 August 1966
Adult	26 August 1966	3400	Observed back 13 September 1966
Yearling	28 May 1967	1100	Not observed again
Yearling	2 June 1968	1700	Not observed again
Yearling	26 August 1966	3400	Observed May 1967 near release site

#### Overlap of home ranges

Seventy-nine percent of adult home ranges (Table 22) did not overlap home ranges of other yearlings or adults (Fig. 22, males 21 to 24 and 9 and 10 etc.).

Ninety-eight percent did not overlap other home ranges of





adults. The one exception, probably the result of my interference, occurred after one (male 10) of two males occupying discrete home ranges (Fig. 22, males 9 and 10) was removed in September 1966. In 1967, the home range of the surviving male overlapped the home range of a new male (Fig. 23, males 9 and 13). In 1968 these two males occupied non-overlapping home ranges.

Table 22. The overlap of home ranges.

Area	Total number of cases	Percent of total cases
Home ranges of adults	52	100
Not overlapping home ranges of either yearlings or adults	41	79
Not overlapping other home ranges of adults	50	98
Home ranges of yearlings	15	100
Not overlapping home ranges of either yearlings or adults	6	40
Overlapping home ranges of adults	8	53
Overlapping other home ranges of yearlings	2	15

Fifty-three percent of the home ranges of yearlings overlapped adult home ranges (Fig. 23, males 25



and 26), while 15 percent overlapped other yearling home ranges (Fig. 25, males 30 and 31). Only 40 percent of yearling home ranges did not overlap other home ranges (Fig. 22, male 10).

#### Size of home ranges

Accurate determination of the size of home range requires enough observations that each additional observation adds less than one percent to the area of the home range (Odum and Kuenzler, 1955). My estimates of home range size are probably minimal as there were never enough observations on individual males to do this. Sizes of home ranges were calculated for each year for each localized male for which there were five or more observations (individual home ranges). No clear relationship between individual home range size and the number of observations was found (Fig. 24), perhaps partly due to variation in size of home ranges. Home ranges appeared to range in size from 0.5 to 8.4 ha.

Home ranges of adults ranged from 0.5 to 7.5 ha and were not significantly different from those of yearlings which ranged from 0.9 to 8.4 ha (Table 23), although the sample size was small for yearlings as most were sighted less than five times. Stoneberg (1967) in Montana found adult home ranges ranged from 1.2 to 6.0 ha but found no localized yearlings. Ellison (1968a) in

Figure 24. The relationship between the size of individual home ranges of adults and yearlings and the number of observations.

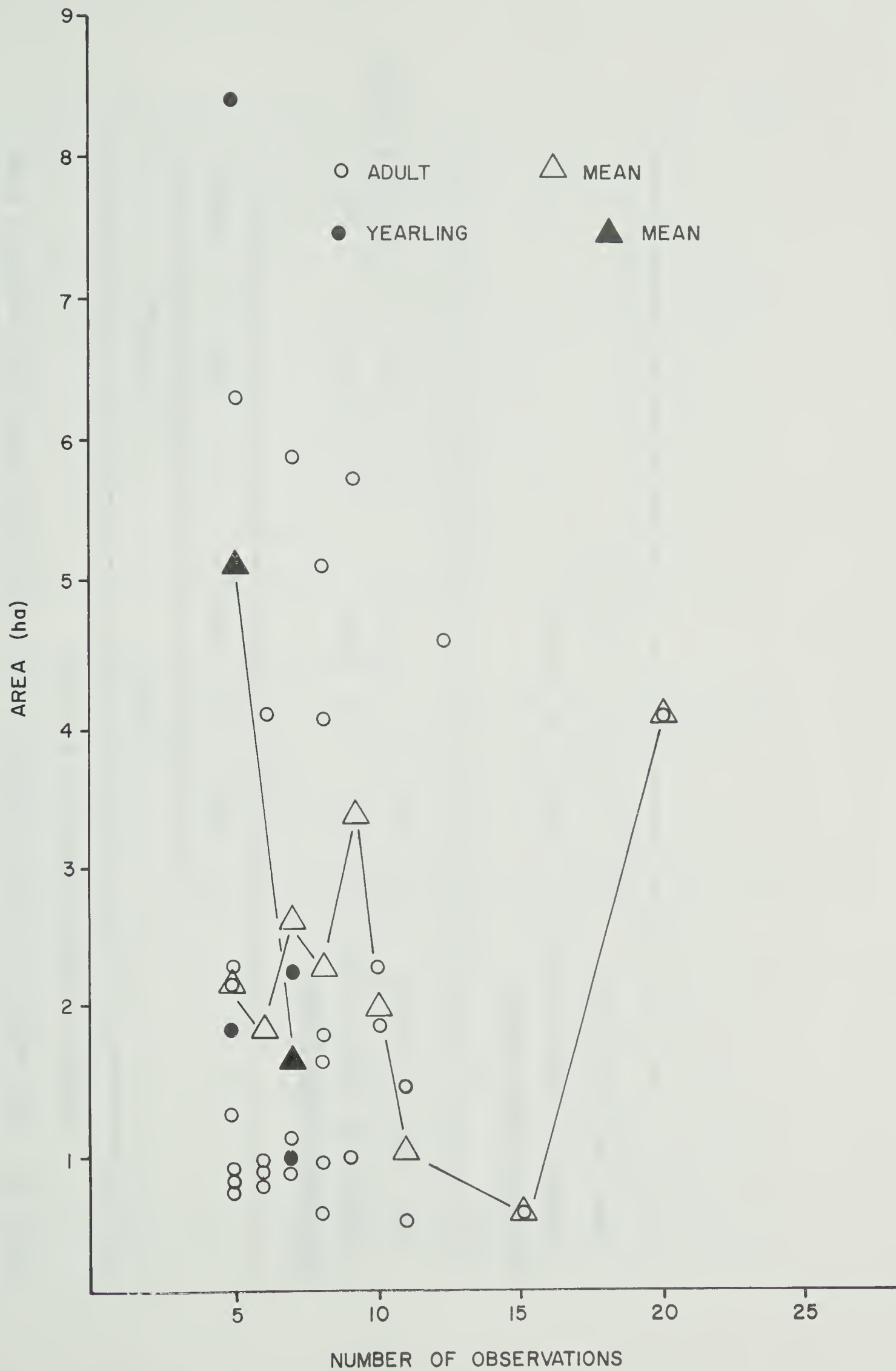






Table 23. The number of observations and size for individual and composite home ranges of male Franklin's grouse.

	Adults				Yearlings			
	$\bar{x}$	$\pm$ SD	n	range	$\bar{x}$	$\pm$ SD	n	range
<u>Individual home ranges</u>								
Number of observations	7.7	$\pm$ 2.9	27	5-20	6.0	$\pm$ 1.2	4	5-7
Home range size (ha)	2.1	$\pm$ 1.7	27	0.5-7.5	3.4	$\pm$ 3.4	4	0.9-8.4
<u>Composite home ranges</u>								
Number of observations	19	$\pm$ 13.2	10	10-52				
Home range size (ha)	2.9	$\pm$ 2.6	10	1.3-10.0				



Alaska found home ranges ranged from 2.0 to 14 ha. These findings generally agree with those of this study.

Stoneberg (1967) calculated home range size by pooling the sighting points of two years for each male (composite home ranges). In this study composite home ranges of from two to four years appeared larger than individual home ranges (Table 23) but the difference was not significant [ $P, 35df, (t\ 0.93) < 0.4$ ]. If home ranges of individual males are static from year to year (and they may not be), the size of composite home ranges might be a more realistic estimate of home range size.

#### Establishment of home ranges

Home ranges of adults were probably established before 1 May, as adults, usually all found by 15 May, were then present on their home ranges.

Yearlings from 1968, when searching was not as thorough, were excluded from consideration here as were yearlings which were transported or killed. Only 45 percent of the yearlings when first observed were localized and fell into the categories "no large movement" and "large movement and return" (Table 24). As they were first observed between 17 May and 13 June, several weeks later than the adults, they may not have occupied home ranges till then, although as they were generally more difficult to find than adults, they may have been



Table 24. Dates for the various types of movement shown by yearling male Franklin's grouse.

Type of movement	Date last observed "wandering"	Date first observed occupying a home range
Yearlings occupying a home range (45%)		May 17
		May 17
		May 18
		May 23
		May 25
		May 28
		June 1
		June 2
		June 4
		June 4
"Wandering" yearlings which were later observed to occupy home ranges (18%)	May 5	July 19
	May 28	July 26
	July 3	July 27
	June 15	August 2
"Wandering only" yearlings (36%)	July 27	
	August 12	
	May 20	
	May 23	
	May 27	
	June 1	
	June 19	
	August 23	



overlooked. Other yearlings (36 percent), last observed between 27 July and 23 August, fell in the categories "large movement and no return" and "observed once and not observed again" and were classified as "wandering only", probably not occupying home ranges during the summer (Table 24). A few yearlings (18%) seemed to wander during May and June, becoming localized and occupying home ranges (at least three observations in a localized area over a period of more than a month and no further "large movement") in the late summer (Fig. 22, male 18).

I believe the next question to ask is whether being present on the study area as a juvenile gave an advantage to a yearling in occupying a home range there. Yearlings banded as yearlings could presumably have come to the study area from elsewhere, but could have been missed as juveniles the preceding year. In 1965 an intense search for juveniles was made in August over the area which later became the main study area. I believe, as does K.H. McCourt (pers. comm.) that many, if not most, of the juveniles on the main study area were banded in 1965 to 1967. Yearlings of 1965 were not considered as there was no opportunity to have banded them as juveniles. Twelve (44 percent) yearlings present on the main study area were banded as juveniles, while 15 (56 percent) were banded as yearlings and could have been newcomers.





Yearlings banded as juveniles did not appear to have any advantage in occupying home ranges although the sample size is very small (Table 25).

Table 25. Summer movements of yearlings banded as juveniles as a proportion of all yearlings.

Type of movement	Percent
Yearlings occupying home ranges	44 (4 of 9)
"Wandering" yearlings which later occupied home ranges	67 (2 of 3)
"Wandering only" yearlings	50 (4 of 8)

#### Change in location of home ranges over winter

As yearlings became young adults in their second fall and older adults in their third, change in location of home ranges over winter by young adults was movement from their home ranges occupied as yearlings (only young adults which occupied home ranges as yearlings were considered). Change by older adults was movement over winter from either their home ranges as young or older adults. I believe these were real changes in location of home ranges as only changes of 250 m or greater were considered, and these changes usually involved crossing a



natural boundary (stream or opening in the forest).

Most older adults showed no change of location of home range over winter while many young adults changed home ranges over winter (Table 26). The types of over-winter movement shown by these two groups of males were significantly different ( $\chi^2(1df)=7.76^*$ ). Male 15, an adult, and male 18, a yearling (Fig. 22 and 23) showed no change of location of their home ranges over winter while male 13, a yearling (Fig. 22 and 23), moved its home range across the creek over winter.

Table 26. Change in location of home ranges over winter by young adult and older adult male Franklin's grouse.

Type of change	Young adults	Older adults
No change in location	2	23
Change in location	5	3

The distances over which adults moved their home ranges (Table 27) are probably minimal, and had the study area been larger, males might have been found to move greater distances.



Table 27. The distances which adults moved their home ranges over winter.

Age group	Distances moved over winter (m)			
	$\bar{x}$	$\pm SD$	n	range
Young adults	428	$\pm 77$	5	340-520
Older adults	917	$\pm 578$	3	250-1280

Bendell and Elliott (1967), working with blue grouse, found that young adults moved over winter from their yearling locations as did Franklin's grouse, while older adult male blue grouse absent from their territories were considered dead. As older male Franklin's grouse occasionally move over winter, an older adult male absent from its home range should not be considered dead although it may be probable.

#### Survival of male Franklin's grouse on the main study area

Three partially eaten birds, killed or scavenged, were found. Goshawks (Accipiter gentilis) and coyotes (Canis latrans) were present on the study area and could have been involved. No trace was found of the other 18 males which disappeared from the study area. As yearlings





wandered during the summer and young and older adults moved over winter, mortality could not be assumed. Estimates of survival of males over winter within the study area population are therefore minimal estimates of true survival. Males killed in handling, removed or lost in experiments were omitted. Survival of young adults, from summer as yearlings over winter till the next spring as young adults, averaged 68 percent over the study while survival of older adults from summer as young or older adults over winter averaged 77 percent, a survival for all ages of 67 percent (Table 28). Over the winter of 1967-8, when the age of all males entering the winter was known, survival was 73 percent for older adults, 45 percent for young adults and for all ages 62 percent. Survival data in the other years, when males of unknown age were present, are less meaningful. As young adults showed greater movement over the winter than older adults, the lower survival of young adults on the main study area is not satisfactory evidence of greater mortality among young adults.

Stoneberg (1967) found that all four older adults survived over one winter while one of two young adults disappeared, results which agree with those of this study. Bendell and Elliott (1967) suggest comparable survival rates of 76 percent for older adult blue grouse



Table 28. Annual survival over winter of male Franklin's grouse on main study area.

Age	Number of males surviving <sup>1</sup> and percent survival		
	1966	1967	1968
Older adult	2(67%)	8(89)%	13(73%)
Young adult	3(75%)	7(100%)	5(45%)
Unknown age	3(33%)	2(67%)	--
All ages	8(50%)	17(89%)	18(62%)
			23(77%)
			16(68%)
			5(42%)
			43(67%)

<sup>1</sup>Survival over winter from previous year.



and 73 percent for young adults.

#### Replacement of missing males

The movement, disappearance, death and removal of males from their home ranges on the total study area presented opportunities to examine replacement. Replacement of males by yearlings (Table 29) occurred on three occasions over the first winter following absence of the original male. One original male, removed in spring, was not replaced over the summer, and another removed in spring was not replaced until over the second winter. In two cases, however, males killed in the spring were replaced by yearlings already present near the home ranges of the original males.

Most replacement was by adults, of which most were young adults (Table 30), but in at least three instances replacement was by an older adult. On the main study area, all replacing young adults had been present there as yearlings. Most missing birds were replaced over the first winter.

Generally, the home ranges of replacing males occupied the same areas as those of their predecessors, particularly if these areas were bounded by natural barriers (streams, hills or openings in the forest). In the absence of such barriers, home ranges of successive males might only overlap.



Table 29. The replacement of males which disappeared, moved, were removed or found dead, by yearling male Franklin's grouse.

Age	Original males			Replacement males	
	Fate	When last observed	Age		When first observed
Adult	Removed	Spring 1965	Yearling		Spring 1967
Adult	Disappeared	Fall 1965	Yearling		Spring 1966
Adult	Removed	Fall 1966	Yearling		Spring 1967
Adult	Removed	Spring 1967	Yearling		Spring 1968
Unknown	Found dead	Spring 1965	Yearling		Spring 1965
Adult	Removed	Spring 1966	2 yearlings		Spring 1966





Table 30. The replacement of males which disappeared, moved, were removed or found dead, by adult and yearling male Franklin's grouse.

Original males				Replacement males	
Age	Fate	When last observed	Age		When first observed
Adult	Disappeared	Fall 1967	Young adult		Spring 1968
Adult	Disappeared	Fall 1967	Young adult		Spring 1968
Adult	Disappeared	Fall 1965	Young adult		Spring 1966
Unknown	Disappeared	Fall 1965	Young adult		Spring 1966
Yearling	Removed	Fall 1966	Young adult		Spring 1967
Adult	Removed	Fall 1966	Older adult		Spring 1967
Adult	Moved	Fall 1967	Older adult		Spring 1968
Adult	Found dead	Spring 1966	Adult		Spring 1967
Adult	Disappeared	Fall 1967	Adult		Spring 1968
Adult	Disappeared	Fall 1967	Adult		Spring 1968
Adult	Disappeared	Fall 1965	Yearling Young adult		Spring 1966 Spring 1967
Two adults	Removed	Fall 1966	Yearling Young adult Older adult		Spring 1967 Spring 1967 Spring 1967



Five males which occupied home ranges and disappeared or moved were not replaced during the study.

Changes in behavior of male Franklin's grouse over the spring and summer

Over the summer, behavior observed for males appeared to change, and, to illustrate this, the behavior of males during the breeding period and in the late summer (15 August to 15 September) were compared. Only three categories of behavioral activities were considered. "Wing-clapping", described by Stoneberg (1967) and MacDonald (1968), is the production of two clapping sounds by the wings at the end of a short flight. "Strutting", first described in detail by Lumsden (1961), was thought by him to be a low intensity aggressive display, while Stoneberg (1967) considered it to be courtship display. "Maintenance behavior" comprised the "normal" and "alert" postures described by Stoneberg (1967). These categories were not mutually exclusive and in any year a male, depending on the activities observed, might fall in one, two or all.

Wing-clapping and strutting were observed for adults predominantly during the breeding period (Table 31). Yearling males with home ranges showed wing-clapping and strutting while wandering yearlings did not. Wing-clapping and strutting were seldom observed in mid-summer



but reappeared in late summer. These observations agree with those of Ellison (1968a) who noted a resurgence of display activity in the fall. As adults outnumbered yearlings by nearly two to one on the main study area, note that a relatively greater proportion of yearlings than adults showed wing-clapping and strutting in the late summer than during the breeding period.

Table 31. Change in behavior of male Franklin's grouse during the breeding period and late summer 1965 to 1968.

Time	Behavior	Age		
		Adults	Yearlings	
			Localized	Wandering
Breeding period	Wing-clapping	38	4	0
	Strutting	47	3	0
	Maintenance behavior	57	7	15
Late summer	Wing-clapping	8	3	0
	Strutting	11	4	0
	Maintenance behavior	42	8	8





Over the summer adult males were observed more often with females than were yearlings (Table 32), most observations occurring in spring. Yearlings, however, were observed with females about equally in spring and summer (with the exception of July) and considering the lower number of yearlings, relatively more yearlings than adults were observed with females in the late summer. Display activity by males with females occurred over the spring and summer although it was generally less intense after the breeding period.

Changes in the area utilized by male Franklin's grouse over spring and summer

Weeden (1965) noted that dispersion might change in two ways: over the season, and during the day. I was able to investigate changes in utilized home range size for adults, but there were too few observations for yearlings.

Dispersion during the breeding period (already defined as 1 May to 15 June) was compared with dispersion over the rest of the summer (16 June to 15 September) by comparing the location of mid-day (900 to 1600 hrs) observations. Mid-day dispersion during the breeding period was compared with evening dispersion (1800 to 2030 hrs) of the breeding period by comparing observations of adult males during these two periods.



Table 32. The number of times males were observed with females over the spring and summer 1965 to 1968.

Month	Number of observations			
	Yearlings		Adults	
	Total	Display activity <sup>1</sup> by male	Total	Display activity by male
May	2	1	14	14
June (1 to 15)	2	2	14	13
June (16 to 30)	-	-	1	1
July	-	-	6	3
August	2	2	4	3
September (1 to 15)	3	2	4	3

<sup>1</sup>Strutting and/or wing-clapping.



The locations of observations for the only adult male studied intensively (Fig. 25) show the area utilized by this male during mid-day of the breeding period to be somewhat smaller than that utilized during mid-day over the rest of the summer. As well, the area utilized by this male in the evening of the breeding period was smaller than that utilized at mid-day of the same period.

Perhaps the problem can be approached in another manner. If the changes described for the one intensively studied male occurred generally, then the distances between successive observations for individual males during the various periods should differ. The distances between successive mid-day observations were significantly smaller for the breeding period (Table 33) than over the rest of the summer [ $P$ , 140 df,  $(t \geq 5.29) \ll 0.05$ ]. Despite the generally greater time between successive observations over the rest of the summer, I believe this is additional evidence that smaller areas are utilized by adults during mid-day of the breeding period than during mid-day over the rest of the summer. The distances between successive observations in the evening of the breeding period (Table 33) were significantly smaller than those of mid-day of the same period [ $P$ , 129 df,  $(t \geq 7.70) \ll 0.05$ ] and is additional evidence of the existence of small areas utilized by adult males in the evening during the breeding

Figure 25. Observations of an adult male Franklin's grouse during  
mid-day and evening over the breeding period and mid-day  
over the rest of the summer 1965 to 1968.

- MID - DAY, BREEDING PERIOD
- MID - DAY, REST OF SUMMER
- EVENING, BREEDING PERIOD







Table 33. Distances between successive observations for individual males during mid-day in the breeding period and over the rest of the summer and in the evening during the breeding period.

Time	Distances in m			
	$\bar{x}$	$\pm SD$	n	range
Daytime <sup>1</sup> , during breeding period <sup>2</sup>	99	$\pm 78$	93	10-383
Daytime, during rest of the summer <sup>3</sup>	237	$\pm 174$	49	10-700
Evening <sup>4</sup> , during breeding period	30	$\pm 25$	38	0-100

<sup>1</sup>900 to 1600 hrs.

<sup>2</sup>1 May to 15 June.

<sup>3</sup>16 June to 15 September.

<sup>4</sup>1800 to 2030 hrs.



period. Display activity by males occurred mostly in the evening and on these small areas, which I called "display areas". The display area in Figure 25 was about 0.4 ha, which I believe to be comparable to other display areas. Occasionally localized yearlings were found to have display areas, but neither their display areas nor display activities were as pronounced as those of adults.

#### Use of the recorded call as a census technique during the breeding period

Stirling and Bendell (1966) described a census method for territorial male blue grouse using a "precopulatory call of the hen" which they estimated was four times as fast and more effective than conventional search. MacDonald (1968) suggested the use of a recorded call of the hen Franklin's grouse, attractive to both males and females, for census purposes.

A census using the female call was done twice on each of three areas of the main study area, each about one square km in area and limited by natural boundaries. Censuses of these areas were done between 900 and 1600 hrs, between 17 May and 16 June, 1968, each taking from four to six hours. Census of each area was also done by conventional search during the regular course of the study.

During the breeding period adult males usually responded to the call played on their home ranges by



approaching and performing display flights and/or strutting, or, if they did not approach, advertized their position with display flights. No adult male found by conventional search and tested with the call ever failed to respond.

Localized yearlings often responded to the call as strongly as adults, but wandering yearlings and some localized yearlings, although they would occasionally approach the call, did not show strutting or display flights. Females attracted to the call often showed the aggressive behavior described by MacDonald (1968).

The first census of the three areas found all the adult males known present, while one adult male was not found on 2 June during the second census (Table 34). The one localized yearling known present was found in both censuses. Only one of the four wandering yearlings and five of the 10 females known present on the census areas were found during the two censuses.

Adult males came to the call 22 times during the first census but only 15 times during the second. The first responses of males were usually strongest, decreasing in later trials, the motivation of the males perhaps lessening as the breeding season advanced, or perhaps as they learned the counterfeit nature of the call. Birds were not found as effectively and generally showed less





Table 34. Results of the census of Franklin's grouse using the recorded call of the female.

	Area 1		Area 2		Area 3		Total for all areas
	19 May <sup>1</sup> 16 June <sup>2</sup>		17 May <sup>1</sup> 21 May <sup>2</sup>		18 May <sup>1</sup> 2 June <sup>2</sup>		First <sup>1</sup> Second <sup>2</sup> census census
Adult males	3(3) <sup>3</sup>	3(3)	4(4)	4(4)	3(3)	2(3)	10(10) 9(10)
Localized yearling male	(0)	(0)	(0)	(0)	1(1)	1(1)	1(1) 1(1)
Wandering yearling males	0(2)	0(2)	1(1)	0(1)	0(1)	0(1)	1(4) 0(4)
Females	2(3)	1(3)	1(4)	0(4)	2(3)	1(3)	5(10) 2(10)

<sup>1</sup>First census using female call.

<sup>2</sup>Second census using female call.

<sup>3</sup>Number of birds found during census with the call; in brackets, the number of birds known present by conventional methods.



intense responses to the call on bright, windy days than on still, overcast days. Perhaps birds did not hear as well in the wind or perhaps there is a psychological or physiological explanation.

I would thus recommend that for greatest efficiency the census be done on cool, still, overcast days, and that to be certain of finding all adult and localized yearling males, it be repeated at least once. The census does not find all wandering yearling males or females, although further repetition might increase the effectiveness for them.

### Territoriality

Tinbergen (1957) defined territory as a defended area, the outcome of two distinct tendencies, "site attachment" and "(intraspecific) hostility". He defined hostility as the outcome of attack and avoidance or escape. As male Franklin's grouse occupy home ranges and fulfill the criterion of "site attachment", it only remains to demonstrate hostility to show them territorial.

Lumsden (1961) with spruce grouse and Stoneberg (1967) and MacDonald (1968) with Franklin's grouse, induced attack using mounted males. I was able to induce eight attacks by adults on a mounted male, but was unable to show attack for localized yearlings (Table 35). The only two localized yearlings present in 1968 were tested,



a small sample on which to base conclusions, particularly as only eight of the 15 trials with adults produced attack.

Table 35. Results of the tests for attack on a mounted male by male Franklin's grouse during the breeding period, 1968.

Age of males	Males tested	Number of trials	Attack observed
Adults	11	15	8
Localized yearlings	2	3	0

Attack on a mounted male generally followed the sequence in Figure 26. Presented with a mounted male, an adult male on its home range responded by calling and by circling in the head-and-tail-down posture (Lumsden, 1961; Stoneberg, 1967; and MacDonald, 1968). After several minutes of calling and circling the male attacked in the head-and-tail-down posture, usually to the front of the mount. Figure 26 shows a frontal attack, the mounted male knocked aside and the attacking male off balance, its tail in a seemingly upright position. The male then attacked the head and combs of the mount, often showing the upright aggressive posture described by

Figure 26. Attack sequence for an adult male Franklin's grouse to a mounted male.

- A - a preliminary threat of circling;
- B - an attack to the front of the mounted male;
- C - pecking attack to the head and combs of the mounted male;
- D - the upright aggressive posture during a pause in the attack on the prostrate mounted male.









Stoneberg (1967).

Nine interactions were observed between males during the course of the study. Attacks were observed only for adults, but as no interactions involving localized yearlings were observed, there was no opportunity to observe possible attack by yearlings. Six interactions involved attack and pursuit of males apparently trespassing on other males' home ranges. The trespassers, both yearlings and adults, retreated from the attacks and left the home ranges of the attacking males. The other three interactions seemed to have occurred on the borders of home ranges or between home ranges, and followed the pattern of mutual threat described by MacDonald (1968). As he noted, after this sort of interaction, males could not be driven across the lines of interaction.

The female call was played 113 times on the main study area in 1967 and 1968, in addition to the 53 times it was played during the census. Although many of the playings were on the edge of or between home ranges, I was never able to attract more than one male to the call at once. When played between home ranges, the resident males which responded generally stayed on their display areas and performed display flights. When played on a home range, the occupant might approach the call but



other localized males which responded remained on their own home ranges and performed display flights. But on five occasions when the call was played beside a home range but not near another home range, the occupant of that home range came up to the call. As neither males nor droppings were found in these areas and the vegetation appeared unsuitable for male Franklin's grouse, I believe these males left their home ranges. I suggest that localized males were conscious of their neighbours and their home ranges and avoided them, but were not adverse to entering unoccupied areas.

Wing-clapping, a characteristic of localized males, was thought by Stoneberg (1967) and MacDonald (1968) to be a territorial advertisement. It may function as a means by which localized males are made aware of and thus are able to avoid one another.

MacDonald (1968), working on the same study area, reported attracting several males at once to the call, resulting in interactions between them. He did this in an area in which four new males had replaced two adults removed the previous fall. Perhaps the home ranges and their boundaries were still in flux, an idea supported by his observations that males would not cross boundary lines established by the interactions.

As adults showed site attachment and hostility



(attack, avoidance and retreat) they were clearly territorial. Wandering yearlings showed retreat but no attack and, lacking home ranges, were not territorial and therefore probably not part of the breeding population. Hostility was neither shown nor its possibility excluded for localized yearlings. As they occupied discrete home ranges, showed display activity and were found with females (similarities to adults), some may have been territorial. But as localized yearling displays were neither as prolonged nor as intense as those of adults, and since their attachment to home ranges may have been lower than that of adults, they were perhaps not the equal of adults in the breeding population. While adult attack may have prevented yearlings from entering the breeding portion of the population, they may simply have been immature, as Bendell and Elliott (1967) suggest is the case for yearling male blue grouse. Settling of wandering yearlings and continued display and association with females by yearlings over the summer can be explained as a gradual maturation during their second summer.

MacDonald (1968) suggested that interactions establish the boundaries of territories and that because territories are so large, these boundaries are linear projections of these interaction points. As few interactions and no boundary patrolling were observed, I





agree. Home range and territory may have been synonymous for adult male Franklin's grouse from May to September, as defense occurred in all months, often on the edges of home ranges. Further, territory and home ranges may not shrink during the breeding period with utilized home range, particularly for the older adults. Three interactions were observed during the breeding period outside the small areas I believed generally occupied at that time. As well, males were occasionally found outside these small areas both during the day and evening of the breeding period. These interpretations differ from those of Stoneberg (1967) who thought males held territories during the spring within larger home ranges occupied in summer.

Site attachment would permit males to become more familiar with the habitat and facilitate finding food and females or avoiding predators. Hostility would enhance dispersion (Tinbergen, 1957) by spacing males as evidenced by their non-overlapping territories, thus filling the available habitat and reducing interactions among males.



PATTERNS OF DISPERSION OF MALE FRANKLIN'S GROUSE AS A  
FUNCTION OF HABITAT

The habitat of the general areas occupied by localized  
males








I described the habitats utilized or not utilized by males, but, as I did not know the significance of the parameters of habitat for the birds, I was unable to identify the means by which males selected habitat. On the main study area, males were found only in lodgepole pine forest, but on the auxiliary study area they were also found in white spruce forest and older mixed forest. Males were never found in meadow or marsh.

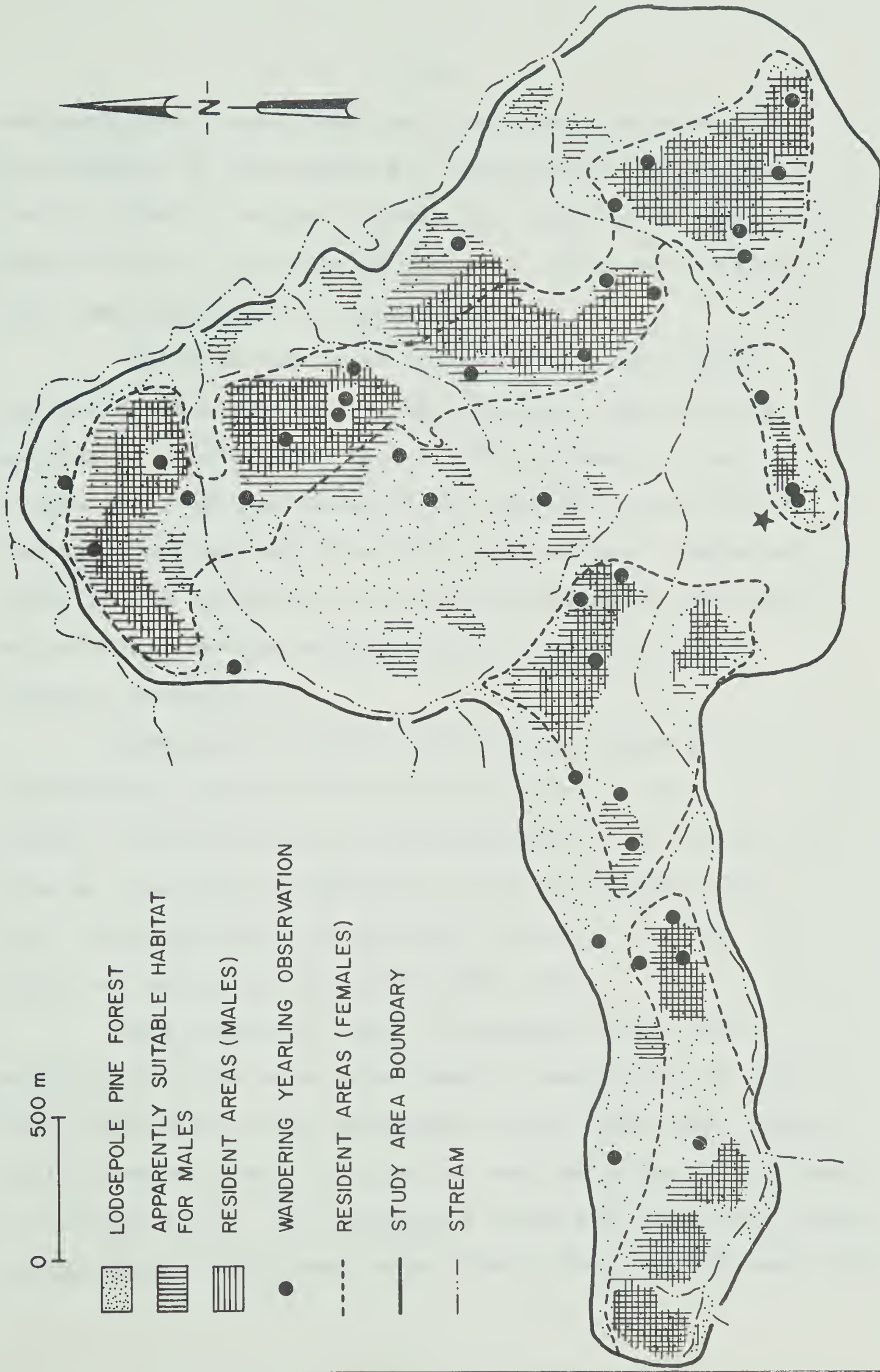
Localized yearlings and adults will be considered "resident males" and the areas of the lodgepole pine forest they occupy will be considered "resident areas" (Fig. 27). These areas constituted only 28 percent of the lodgepole pine forest of the main study area. The additional portion of the lodgepole pine forest of the main study area will be considered "peripheral areas". Wandering yearlings were found on both resident and peripheral areas (Fig. 27).

Of the 225 random plots describing the lodgepole pine forest, 76 fell in the resident areas. The manner in which the cover values for the overstory of resident

Figure 27. Areas occupied by Franklin's grouse on the main study area (1965-1968). The star designates an area occupied 1965-6 but not occupied 1967-8.

0 500 m

-  LODGEPOLE PINE FOREST
-  APPARENTLY SUITABLE HABITAT FOR MALES
-  RESIDENT AREAS (MALES)
-  WANDERING YEARLING OBSERVATION
-  RESIDENT AREAS (FEMALES)
-  STUDY AREA BOUNDARY
-  STREAM







and peripheral areas, and for other comparisons as well, are compared by chi-square for independence (Steel and Torrie, 1960) is shown in Table 36. Results of such comparisons are shown as in Table 37, while the data for such comparisons are in Appendixes 5 to 16.

The overstory cover of lodgepole pine, willow and all species combined of the resident areas was significantly greater than that of the peripheral areas (Table 37). Willow, however, was present on relatively few plots and did not have high cover values. Overstory cover of the resident areas for both lodgepole pine and all species combined was generally between 26 and 75 percent (Appendix 5).

Middlestory cover of the resident areas was significantly greater for willow yet less for all species combined than for the peripheral areas (Table 37). From my experience, middlestory cover was usually less when overstory cover was greater, probably as less light was available for middlestory plants.

Stem diameters (dbh) of lodgepole pine, white spruce and willow were significantly smaller on the resident areas than on the peripheral areas (Table 38). This table, however, does not show the most noticeable differences in the two areas. The peripheral areas were generally on the higher slopes where trees were often either few and very large





Table 36. Example showing the method of statistical comparison of the overstory cover for the resident areas (based on 76 random plots) and the peripheral areas (based on 149 random plots).

Cover <sup>1</sup> value	White spruce		Lodgepole pine		Balsam poplar		Aspen		Willow		Total for all species combined	
	R <sup>2</sup>	P <sup>3</sup>	R	P	R	P	R	P	R	P	R	P
6												
5			1	2							2	3
4			29	13							32	21
3		2	41	52							39	50
2	5	24	4	66		1	1	1		1	3	64
1	34	55	1	14	2	3	1	1	26	28		10
0	37	68		2	74	145	74	147	50	120		1
<hr/>												
$\chi^2$ tabled												
0.05(df)	5.99(2)		7.81(3)		3.84(1)		3.84(1)		3.84(1)		5.99(2)	
$\chi^2$ calculated	5.19		56.7*		0.17		0.02		5.15*		52.8*	

\*Statistically significant.

<sup>1</sup>6=<95-100%, 5=<75-95%, 4=<50-75%, 3=<25-50%, 2=<5-25%, 1=present~5%, 0=absent.

<sup>2</sup>Random plots from the resident areas.

<sup>3</sup>Random plots from the peripheral areas.



Table 37. Statistical comparison of the distribution of cover values for vegetation on 76 random plots in the resident areas and 149 random plots on the peripheral areas.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance
White spruce	5.99(2)	5.19	3.84(1)	3.04
Lodgepole pine	7.81(3)	56.7*	3.84(1)	1.66
Balsam poplar	3.84(1)	0.17	3.84(1)	0.02
Aspen	3.84(1)	0.02	3.84(1)	0.00
Willow	3.84(1)	5.15*	3.84(1)	15.3* +
Alder			5.99(2)	5.71
Dwarf birch			3.84(1)	0.39
Shrubby cinquefoil			3.84(1)	0.38
Rose			3.84(1)	0.87
Buffalo berry			3.84(1)	2.19
Total for all species combined	5.99(2)	58.2* +	7.81(3)	14.5* -

\* Statistically significant; + = greater cover in random plots from resident areas;  
- = less cover in random plots from resident areas.



Table 38. Statistical comparison of stem diameters (dbh) for the resident areas (based on 76 random samples) and the peripheral areas (based on 149 random samples).

Stem diameter Class cm	White spruce		Lodgepole pine		Balsam poplar		Aspen		Willow	
	R <sup>1</sup>	P <sup>2</sup>	R	P	R	P	R	P	R	P
>18-20		1	1	3						
>16-18				9						
>14-16			15	44						
>12-14		1	22	47						
>10-12		1	127	179						
>8-10		2	345	364						
>6- 8	1	9	454	389			4	1	1	1
>4- 6	3	23	473	361			2	1	1	10
>2- 4	29	91	458	387	1		1	13	57	57
>0- 2	58	116	306	331	3	2	3	122	204	204
$\chi^2_{0.05} \text{ tabled}$	5.99(2)		15.5(8)		3.84(1)		3.84(1)		3.84(1)	
$\chi^2_{\text{calculated}}$	10.2*		67.2*		0.15		2.17		10.3*	

\* Statistically significant.  
1 Random plots from the resident areas.  
2 Random plots from the peripheral areas.





or many and very small. These differences are not distinguished in the table, although it can be seen that relatively more large trees were present in the peripheral areas.

Stem density of lodgepole pine and all species combined was significantly greater on the resident areas than on the peripheral areas (Table 39). On the resident areas, lodgepole pine averaged 29 stems per plot and all species combined averaged 33 while on the peripheral areas lodgepole pine and all species combined averaged 14 and 18 stems per plot respectively.

Canopy height was significantly greater in the resident areas averaging 8.2 m as opposed to 7.2 m in the peripheral areas (Table 39). Slope of the forest floor was significantly less in the resident areas than in the peripheral areas which were generally the upper slopes of the hills where greater exposure, drainage and thinner soil probably contributed greatly to differences in vegetative cover and density (Table 39).

Resident male Franklin's grouse seemed to choose habitat in the lodgepole pine forest which had greater overstory cover, less middlestory cover, greater stem density, greater canopy height and lower slope of the forest floor. Figures 4 to 7 show typical habitat of the resident areas, while Figures 9 to 11 show typical



Table 39. Statistical comparison of stem density, canopy height and slope of the forest floor for the resident areas (based on 76 random samples) and the peripheral areas (based on 149 random samples).

Area	White spruce	Lodgepole pine	Willow	Total for all species combined	Canopy height (m)	Slope (degrees)
Resident areas	$\bar{x}$	29	5.5	33	8.2	6.6
	$\pm$ SD	$\pm$ 17	$\pm$ 3.2	$\pm$ 18	$\pm$ 0.8	$\pm$ 4.6
	n	76	22	76	76	76
	range	1-84	1-12	10-84	5-11	1-19
Peripheral areas	$\bar{x}$	14	7.8	18	7.2	10
	$\pm$ SD	$\pm$ 16	$\pm$ 6.0	$\pm$ 17	$\pm$ 2.0	$\pm$ 6.2
	n	149	33	149	149	149
	range	0-108	1-27	1-108	0-11	1-33
t tabled 0.05(df)	1.98(118)	1.96(223)	2.00(53)	1.96(223)	1.96(223)	1.96(223)
t calculated	0.70	11.9*	1.07	6.47*	5.72*	5.11*

\* Statistically significant



habitat of the peripheral areas. The habitat shown in Figure 8 is of intermediate quality which would only be occupied if part of other more suitable habitat. On a typical hillside of the main study area (Fig. 28) the thickly forested resident area is in contrast to the more open peripheral area on the higher slopes.

I believe males which selected thick lodgepole pine forest rather than more open forest would be better sheltered from the inclemencies of weather. In addition, Franklin's grouse utilize pine needles as food (Jonkel and Greer, 1963) and may select the thicker habitat as a food source. Goshawks were often seen flying over the lodgepole pine forest and were occasionally seen in the forest. I believe grouse in the thicker forest would be more difficult for these and other predators to find and attack. In my experience, the light and dark coloration of males is very cryptic in the shadows and sunflecks of the thick lodgepole pine forest.

Stoneberg (1967) found that males occupied home ranges in "medium" and "thick" lodgepole pine forest, but were never found in "open" lodgepole pine forest, results which generally agree with those found in this study.

Figure 28. A hillside on the main study area showing differences in vegetation density and cover of resident and peripheral areas. Resident area outlined in white.









### Natural boundaries as limitations to home ranges

Natural boundaries (openings in the forest, high hills, stream beds and other types of vegetation) often seemed to form the boundaries of home ranges. Generally, resident males observed natural boundaries but yearlings did not (Table 40). The four areas utilized as home ranges over three years of the study shown in Figure 29 did not extend across the natural boundaries formed by stream beds and openings in the forest.

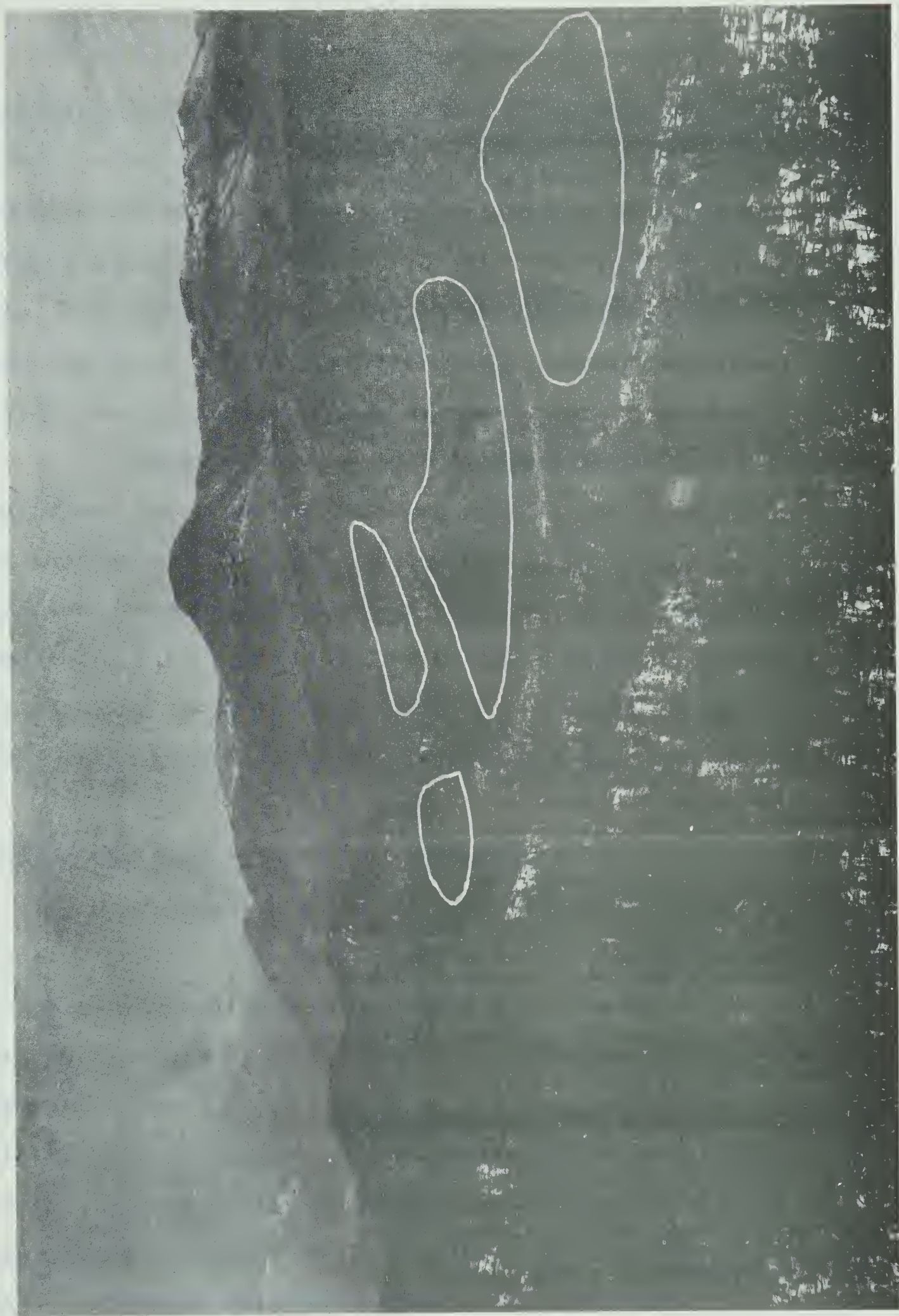
Table 40. Limitations to home ranges set by natural boundaries.

Status of male	Natural boundaries	
	Not crossed	Crossed
Resident males	55	4
Wandering yearling males	2	8

### Size of the vegetation block

On the main study area I located a number of areas of apparently suitable habitat in which resident males were never observed (Fig. 27). These areas were usually smaller than home ranges. As well, home ranges and

Figure 29. A hillside on the main study area showing natural boundaries delineating the shape and size of home ranges. Areas occupied by home ranges outlined in white.







resident areas usually had zones of apparently suitable habitat about them. Males which disappeared or moved and were not replaced generally occupied home ranges in smaller blocks of habitat. The small block of vegetation (Fig. 27, star) occupied in 1965 and 1966 by an adult male lay empty in 1967 and 1968. Replacement occurred rapidly in the larger blocks of vegetation.

I suggest that unless suitable habitat is in a contiguous block of some minimum size, it will not be utilized by resident male Franklin's grouse or, if utilized, replacement will not occur quickly. My experience with replacement on the main study area and in searching for males elsewhere in the Sheep Valley would place this minimum size at about 2 ha.

#### Habitat utilized by specific groups of males

Male Franklin's grouse were classified into four groups: adults; localized yearlings; wandering yearlings on the resident areas; and wandering yearlings on the peripheral areas. Since habitat was measured in terms of vegetative cover at the sites of all observations of males, the descriptions of the habitats utilized by the groups of males could be compared with each other and with the descriptions of the resident and peripheral areas. Although the sample sizes for some of these





groups are small, because the analyses were done for a number of males at different times during the spring and summer, I believe they represent the habitats utilized by these groups of males.

The overstory cover for lodgepole pine and for all species combined was significantly greater in the habitats utilized by adults than in the resident areas generally (Table 41). Perhaps, as has already been suggested generally for resident males in the lodgepole pine forest, adult males may select thicker forest in the resident areas for food and shelter. The middlestory cover in the habitat utilized by adults was significantly less for willow and rose than on the resident areas generally (Table 41), perhaps due to the greater overstory cover utilized by adults.

The overstory cover of the habitat utilized by localized yearlings was significantly greater for aspen than on the resident areas generally (Table 42), although aspen was present on few plots at low cover values (Appendices 5 to 8). There was no significant difference for lodgepole pine and all species combined. Middlestory cover was significantly greater for white spruce, aspen, willow, shrubby cinquefoil, buffalo berry and all species combined in the habitat utilized by localized yearlings than in the resident areas generally (Table 42). White



Table 41. Statistical comparison of the cover values for the 76 random plots from the resident areas and for 227 sites where adult males were observed.

Species	Overstory $\chi^2$		Abun-		Middlestory $\chi^2$		Abun-
	$\chi^2$ tabled -	0.05 (df)	calculated	dance	$\chi^2$ tabled -	0.05 (df)	dance
White spruce	5.99(2)	3.17			3.84(1)	0.00	
Lodgepole pine	7.81(3)	9.95*	+		3.84(1)	0.05	
Balsam poplar	3.84(1)	0.33			3.84(1)	0.06	
Aspen	3.84(1)	1.53			3.84(1)	0.03	
Willow	3.84(1)	0.59			5.99(1)	20.1*	-
Alder					5.99(2)	3.08	
Dwarf birch					3.84(1)	1.23	
Shrubby cinquefoil					3.84(1)	1.55	
Rose					3.84(1)	4.36*	-
Buffalo berry					3.84(1)	0.56	
Total for all species combined	7.81(3)	11.0*	+		7.81(3)	4.94	

\* Statistically significant; + = greater at the sites where adult males were observed;  
 - = less at the sites where adult males were observed.



Table 42. Statistical comparison of the cover values for 57 sites where localized yearling males were observed and the 76 random plots from the resident areas.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated
White spruce	3.84(1)	0.14	3.84(1)	5.62*
Lodgepole pine	3.84(1)	0.00	3.84(1)	2.06
Balsam poplar	3.84(1)	2.33	3.84(1)	0.06
Aspen	3.84(1)	8.46*	5.99(2)	7.19*
Willow	3.84(1)	0.02	3.84(1)	18.0*
Alder			5.99(2)	1.16
Dwarf birch			3.84(1)	0.85
Shrubby cinquefoil			3.84(1)	6.11*
Rose			3.84(1)	0.77
Buffalo berry			3.84(1)	5.37*
Total for all species combined	3.84(1)	0.11	5.99(2)	11.6*

\* Statistically significant: + = greater at the sites where localized yearling males were observed.



spruce and willow were present on the most plots and had the greatest cover values (Appendices 5 and 8).

When the habitat utilized by yearlings is compared with that utilized by adults (Table 43) the overstory cover of white spruce, aspen and balsam was significantly greater in the habitat utilized by localized yearlings. In the middlestory, the cover for white spruce, aspen, rose, buffalo berry and all species combined was significantly greater in the habitat utilized by localized yearlings. White spruce and willow were present on the most plots and had the highest cover values (Appendices 7 and 8).

Dependent on the initial assumptions, several explanations are possible for the habitat utilized by localized yearlings. If it were true that the most suitable habitat for adults were also the most suitable habitat for localized yearlings, then it would follow that localized yearlings did not utilize optimum habitat. Yearlings might do this if they were less familiar with their home ranges than were adults, or if they were unable to distinguish between more and less favourable habitats to the same extent as were adults. As adults were found to defend their territories against yearlings, another possible explanation might be that yearlings were obliged to seek greater middlestory cover to avoid adults.





Table 43. Statistical comparison of the cover values for 57 sites where localized yearling males were observed and 227 sites where adult males were observed.

Species	Overstory		Middlestory		Abun-
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	
White spruce	3.84(1)	3.90*	3.84(1)	8.13*	+
Lodgepole pine	7.81(3)	3.22	3.84(1)	2.19	
Balsam poplar	3.84(1)	12.1*	3.84(1)	0.14	
Aspen	3.84(1)	5.88*	3.84(1)	15.3*	+
Willow	3.84(1)	0.07	5.99(2)	5.59	
Alder			5.99(2)	0.86	
Dwarf birch			3.84(1)	0.07	
Shrubby cinquefoil			3.84(1)	3.39	
Rose			3.84(1)	11.3*	+
Buffalo berry			3.84(1)	8.95*	+
Total for all species combined	5.99(2)	1.83	5.99(2)	9.69*	+

\* Statistically significant; + = greater at the sites where localized yearling males were observed.



If localized yearlings were not mature or the equal of adults in the breeding population, perhaps localized yearlings, not as concerned with territorial or breeding activities as adults, might find relatively better protection and survival in habitat of greater middlestory cover.

No significant differences were found when habitat utilized by wandering yearlings on the resident areas was compared with that of the resident areas (Table 44), that utilized by adults (Table 45), or that utilized by localized yearlings (Table 46).

Yearlings wandering on the peripheral areas utilized habitat of significantly greater overstory cover than on the peripheral areas generally for lodgepole pine and all species combined (Table 47), perhaps utilizing the thicker forest for food and shelter. The habitat utilized by these yearlings was not significantly different from that of the resident areas (Table 48) or that utilized by wandering yearlings in the resident areas (Table 49) but had significantly less overstory cover for lodgepole pine and all species combined than that utilized by adults (Table 50), and significantly less middlestory cover than that utilized by localized yearlings (Table 51).



Table 44. Statistical comparison of the cover values for 17 sites where wandering yearlings of the resident areas were observed and the 76 random plots from the resident area.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance
White spruce	3.84(1)	0.21	3.84(1)	1.61
Lodgepole pine	3.84(1)	0.00	3.84(1)	0.16
Balsam poplar	3.84(1)	0.06	3.84(1)	0.06
Aspen	3.84(1)	1.03	3.84(1)	0.19
Willow	3.84(1)	0.32	3.84(1)	0.09
Alder			3.84(1)	2.25
Dwarf birch				
Shrubby cinquefoil			3.84(1)	0.68
Rose			3.84(1)	0.82
Buffalo berry			3.84(1)	0.00
Total for all species combined	3.84(1)	0.01	3.84(1)	0.05





Table 45. Statistical comparison of the cover values for 17 sites where wandering yearlings of the resident areas were observed and 227 sites where adult males were observed.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	Abun- $\chi^2$ calculated
White spruce	3.84(1)	0.56	3.84(1)	1.97
Lodgepole pine	3.84(1)	1.23	3.84(1)	0.07
Balsam poplar	3.84(1)	1.01	3.84(1)	0.44
Aspen	3.84(1)	0.02	3.84(1)	0.23
Willow	3.84(1)	0.03	3.84(1)	0.29
Alder			3.84(1)	0.56
Dwarf birch			3.84(1)	0.00
Shrubby cinquefoil			3.84(1)	0.03
Rose			3.84(1)	0.00
Buffalo berry			3.84(1)	0.10
Total for all species combined	3.84(1)	0.50	3.84(1)	0.05



Table 46. Statistical comparison of the cover values for 17 sites where wandering yearlings of the resident areas were observed and 57 sites where localized yearlings were observed.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.04 (df)	Abun- $\chi^2$ calculated
White spruce	3.84(1)	0.00	3.84(1)	0.04
Lodgepole pine	3.84(1)	0.01	3.84(1)	0.00
Balsam poplar	3.84(1)	0.79	3.84(1)	0.42
Aspen	3.84(1)	0.12	3.84(1)	1.79
Willow	3.84(1)	0.11	3.84(1)	0.04
Alder			3.84(1)	1.14
Dwarf birch			3.84(1)	0.00
Shrubby cinquefoil			3.84(1)	0.01
Rose			3.84(1)	2.13
Buffalo berry			3.84(1)	2.11
Total for all species combined	3.84(1)	0.01	3.84(1)	1.85



Table 47. Statistical comparison of the cover values for 21 sites where wandering yearlings on the peripheral area were observed and the 149 random plots for the peripheral areas.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	Abun- $\chi^2$ calculated dance
White spruce	3.84(1)	0.17	3.84(1)	1.26
Lodgepole pine	3.84(1)	5.99*	3.84(1)	0.04
Balsam poplar	3.84(1)	0.00	3.84(1)	0.09
Aspen	3.84(1)	0.30	3.84(1)	0.66
Willow	3.84(1)	0.03	3.84(1)	0.02
Alder			3.84(1)	0.58
Dwarf birch			3.84(1)	0.05
Shrubby cinquefoil			3.84(1)	0.05
Rose			3.84(1)	1.87
Buffalo berry			3.84(1)	0.01
Total for all species combined	3.84(1)	8.24*	3.84(1)	2.15

\* Statistically significant; + = greater at the sites where wandering yearlings on the peripheral area were observed.



Table 48. Statistical comparison of the cover values for 21 sites where wandering yearlings on the peripheral areas were observed and the 76 random plots from the resident areas.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated
White spruce	3.84(1)	0.38	3.84(1)	0.00
Lodgepole pine	3.84(1)	1.12	3.84(1)	0.46
Balsam poplar	3.84(1)	0.01	3.84(1)	0.01
Aspen	3.84(1)	0.01	3.84(1)	0.42
Willow	3.84(1)	0.41	3.84(1)	1.08
Alder			3.84(1)	0.00
Dwarf birch				
Shrubby cinquefoil				
Rose			3.84(1)	3.15
Buffalo berry			3.84(1)	1.51
Total for all species combined	3.84(1)	1.17	3.84(1)	0.05





Table 49. Statistical comparison of the cover values for 21 sites where wandering yearlings on the peripheral areas were observed and 17 sites where wandering yearlings on the resident area were observed.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated dance	$\chi^2$ tabled - 0.05 (df)	Abun- $\chi^2$ calculated dance
White spruce	3.84(1)	0.05	3.84(1)	0.65
Lodgepole pine	3.84(1)	0.17	3.84(1)	0.09
Balsam poplar				
Aspen	3.84(1)	0.78	3.84(1)	0.01
Willow	3.84(1)	0.15	3.84(1)	0.37
Alder			3.84(1)	0.89
Dwarf birch				
Shrubby cinquefoil			3.84(1)	0.01
Rose			3.84(1)	1.01
Buffalo berry			3.84(1)	1.04
Total for all species combined	3.84(1)	0.70	3.84(1)	0.01



Table 50. Statistical comparison of the cover values for 21 sites where wandering yearlings on the peripheral areas were observed and 227 sites where adult males were observed.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	Abun- calculated dance
White spruce	3.84(1)	2.78	3.84(1)	0.00
Lodgepole pine	3.84(1)	5.20*	3.84(1)	0.29
Balsam poplar	3.84(1)	0.71	3.84(1)	0.26
Aspen	3.84(1)	0.72	3.84(1)	0.46
Willow	3.84(1)	0.05	3.84(1)	0.05
Alder			3.84(1)	0.24
Dwarf birch			3.84(1)	0.02
Shrubby cinquefoil			3.84(1)	0.05
Rose			3.84(1)	0.99
Buffalo berry			3.84(1)	1.69
Total for all species combined	3.84(1)	6.07*	3.84(1)	0.17

\*Statistically significant; - = less at the sites where yearlings wandering on the peripheral areas were observed.



Table 51. Statistical comparisons of the cover values for 21 sites where wandering yearlings on the peripheral areas were observed and 57 sites where localized yearlings were observed.

	Overstory		Middleground	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated
White spruce	3.84(1)	0.04	3.84(1)	1.83
Lodgepole pine	3.84(1)	1.18	3.84(1)	0.01
Balsam poplar	3.84(1)	1.14	3.84(1)	0.27
Aspen	3.84(1)	3.26	3.84(1)	4.73*
Willow	3.84(1)	0.16	3.84(1)	2.58
Alder			3.84(1)	0.01
Dwarf birch			3.84(1)	0.00
Shrubby cinquefoil			3.84(1)	1.14
Rose			3.84(1)	5.25*
Buffalo berry			3.84(1)	0.00
Total for all species combined	3.84(1)	1.87	3.84(1)	4.17*

\* Statistically significant; - = less at the sites where yearlings wandering on the peripheral areas were observed.





As adults defended their territories against yearlings, the territorial activity of adults may have caused wandering yearlings to avoid the resident areas. But many yearlings found wandering on the peripheral areas were later observed on the resident areas, often becoming localized there as yearlings or young adults. While yearling Franklin's grouse may be attracted to adult males and their territories as Gullion (1967) suggested for ruffed grouse, I suggest at least part of the attraction of the resident areas for wandering males is the suitable habitat there. Further, I believe wandering by yearlings generally is at least partly directed toward finding suitable habitat.

Resident males showed a generally clumped pattern of dispersion in the lodgepole pine forest. Gullion (1967) suggested clumping in ruffed grouse was due to a lek pattern, an idea which Ellison (1968a, p. 8) rejected as an explanation for the dispersion of spruce grouse which he considered "one of defense of relatively large and individual sites that are often widely spaced". I agree with Ellison and suggest that the clumped dispersion of male Franklin's grouse on the main study area is best explained by habitat availability and selection.

Robinson (1969) showed habitat selection for spruce grouse in northern Michigan, although the results



are not directly comparable with the results of this study, as he considered all age groups of both sexes together.

Habitat utilized as display areas during the breeding period

Stoneberg (1967) found that during the breeding season males displayed in small openings of the lodgepole pine forest, while Ellison (1968a) found "drumming flights" were performed in small openings in the forest. I found that males occupied small display areas in the evening of the breeding period (1 May to 15 June) and often displayed there. Ten random plots from one of these display areas were compared with 18 random plots from the rest of the home range in terms of cover, stem diameter, stem density and canopy height.

Overstory cover for lodgepole pine and all species combined was significantly less on the display area than over the rest of the home range (Table 52). No significant differences were found in middlestory of the two areas.

Stem diameters (dbh) were significantly larger for the lodgepole pine stems but significantly smaller for white spruce of the display area than over the rest of the home range (Table 53). This had the effect of



Table 52. Statistical comparison of the cover values for 10 random plots from a display area and 18 random plots from the rest of the home range.

Species	Overstory		Middlestory		Abund
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	
White spruce	3.84(1)	0.00	3.84(1)	0.00	
Lodgepole pine	3.84(1)	4.93*	3.84(1)	0.30	
Balsam poplar					
Aspen					
Willow	3.84(1)	1.40	3.84(1)	0.94	
Alder			3.84(1)	0.32	
Dwarf birch					
Shrubby cinquefoil					
Rose					
Buffalo berry			3.84(1)	0.11	
Total for all species combined	3.84(1)	3.88*	3.84(1)	0.29	

\* Statistically significant; - = less on the plots from the display area.



Table 53. Statistical comparison of stem diameters (dbh) for a display area (based on 10 random samples) and the rest of the home range (based on 18 random samples).

Tree diameter class cm	White spruce		Lodgepole pine		Willow	
	RA <sup>1</sup>	RB <sup>2</sup>	RA	RB	RA	RB
>16-18				1		
>14-16			5	2		
>12-14			15	12		
>10-12		1	18	53		
>8-10		2	30	108		
>6- 8	1	6	29	145		1
>4- 6	2	6	32	136		
>2- 4	7	7	8	75	1	11
>0- 2	6	2	5	25		9
$\chi^2$ tabled 0.05 (df)	3.84(1)		9.49(4)		3.84(1)	
$\chi^2$ calculated	5.28*		24.8*		0.13	

\* Statistically significant.  
 1 Random plots from the display area.  
 2 Random plots from the rest of the territory.





opening the area between the middlestory and the canopy of the display area.

Stem density was significantly less on the display area than over the rest of the home range for lodgepole pine and all species combined, also resulting in a more open area between the middlestory and the canopy (Table 54). No significant difference was found in the canopy heights of the two areas (Table 54).

Stoneberg (1967) and MacDonald (1968) describe the flight displays of Franklin's grouse. I suggest that males utilized the more open areas of their home ranges for display areas as the lower stem density and absence of smaller trees would facilitate display flights. As well, the lower overstory coverage, allowing more light to enter the forest, would facilitate visibility and evening display activity. Figure 11 shows the open habitat of a display area, while Figures 8 to 10 show some areas on home ranges which were not utilized as display areas. Although most adults used open areas for display areas, some home ranges did not have open areas and display was in the thick forest.

#### Habitat utilized during moult

Male Franklin's grouse begin moulting in mid-June, renewing their plumage by October. During the



Table 54. Statistical comparison of stem density and canopy height for a display area (based on 10 random samples) and the rest of the home range (based on 18 random samples).

Area	Density		Canopy height
	Lodgepole pine	Total for all species combined	
Random plots	$\bar{x}$ 13.4	17.0	7.60
from display	$\pm$ SD $\pm$ 10.1	$\pm$ 6.83	$\pm$ 2.88
area	n 10	10	10
	range 7-20	9-35	5-10
Random plots	$\bar{x}$ 31.1	34.3	8.51
from the	$\pm$ SD $\pm$ 14.2	$\pm$ 14.5	$\pm$ 1.48
rest of the	n 18	18	18
home range	range 13-59	14-63	6-10
t tabled 0.05 (df)	2.06(26)	2.06(26)	2.06(26)
t calculated	5.56*	4.34*	1.56

\* Statistically significant.



period when rectrices are absent and moulting is at its height (conservatively estimated as 10 July to 20 August), males were found at less than half the spring rate. At this time, in contrast to the usual fearlessness of Franklin's grouse, the reaction of males to an observer was often one of fear, characterized by running or flying wildly.

The overstory cover of the habitat utilized by males during this moulting period was significantly greater for white spruce while the middlestory cover was significantly greater for willow, alder and all species combined when compared to the habitat utilized during the breeding period (Table 55). As the deciduous species were in leaf in mid-summer, but were hibernial or budding for much of the breeding period, the real differences in cover utilized during these two periods are much greater.

If the increased wariness of males to observers during moult could be interpreted as generally increased wariness and if incomplete plumage makes males more vulnerable to predators, as their behavior might indicate, then males may have utilized the denser habitat near the ground for shelter from potential predators.

Ellison (1968a) noted movement of males into other vegetation types to pass the period of moult.





Table 55. Statistical comparison of the cover values for 128 sites where adults were observed during the breeding period and 37 analyses at the point of sighting of adult males during the moulting period.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	Abun- calculated dance
White spruce	3.84(1)	3.97*	3.84(1)	0.01
Lodgepole pine	3.84(1)	0.76	3.84(1)	0.02
Balsam poplar	3.84(1)	0.01	3.84(1)	3.21
Aspen	3.84(1)	0.23	3.84(1)	0.38
Willow	3.84(1)	1.94	5.99(2)	17.5* +
Alder			5.99(2)	11.5* +
Dwarf birch			3.84(1)	0.01
Shrubby cinquefoil			3.84(1)	0.31
Rose			3.84(1)	1.48
Buffalo berry			3.84(1)	2.55
Total for all species combined	5.99(2)	5.62	3.84(1)	37.4* +

\* Statistically significant; + = greater at the sites where adults were observed during the moulting period.



The habitat utilized by males in relation to that utilized by female Franklin's grouse

Over the spring and summer females appeared to have a less restricted habitat than resident males on the main study area (Fig. 27). Yearling and adult females were pooled as both breed (McCourt, 1969). Adult males utilized habitat of significantly greater overstory for lodgepole pine and all species combined, but significantly less for white spruce and balsam poplar than females (Table 56). The middlestory cover for white spruce, balsam poplar, aspen, willow, shrubby cinquefoil, rose, buffalo berry and all species combined was also significantly less in habitat utilized by males. McCourt (pers. comm.) thought much of the difference was due to the more open overstory and denser middlestory utilized by females with broods.

During the breeding period (1 May to 15 June) adult males utilized habitat of significantly less overstory for white spruce and balsam poplar and significantly less middlestory for rose, buffalo berry and all species combined (Table 57). As adult males were observed most often with females during the breeding period and the differences in habitats utilized by the two sexes were smaller, the dispersion of females was probably more restricted during the breeding period and the spatial separation of the sexes probably less.



Table 56. Statistical comparison of the cover values at 227 sites where adult males were observed and 215 sites where females were observed.

Species	Overstory		Middlstory		Abun-
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated	
White spruce	5.99(2)	9.67*	5.99(2)	8.37*	-
Lodgepole pine	9.49(4)	76.4*	3.84(1)	1.10	+
Balsam poplar	3.84(1)	17.0*	3.84(1)	11.6*	-
Aspen	3.84(1)	0.02	3.84(1)	12.9*	-
Willow	3.84(1)	0.32	9.49(4)	41.4*	-
Alder			5.99(2)	3.01	
Dwarf birch			3.84(1)	1.12	
Shrubby cinquefoil			3.84(1)	19.0*	-
Rose			3.84(1)	27.9*	-
Buffalo berry			3.84(1)	29.9*	-
Total for all species combined	7.81(3)	22.2*	9.49(4)	51.6*	-

\* Statistically significant; + = greater at the sites where adult males were observed,  
 - = less at the sites where adult males were observed.



Table 57. Statistical comparison of the cover values for 128 sites where males were observed and 80 sites where females were observed during the breeding period.

Species	Overstory		Middlestory	
	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance	$\chi^2$ tabled - 0.05 (df)	$\chi^2$ calculated Abun- dance
White spruce	5.99(2)	13.8*	3.84(1)	0.27
Lodgepole pine	7.81(3)	6.38	3.84(1)	0.02
Balsam poplar	3.84(1)	4.53*	3.84(1)	1.14
Aspen	3.84(1)	0.53	3.84(1)	0.19
Willow	3.84(1)	0.17	5.99(2)	2.27
Alder			5.99(2)	0.32
Dwarf birch			3.84(1)	0.17
Shrubby cinquefoil			3.84(1)	3.13
Rose			3.84(1)	12.3*
Buffalo berry			3.84(1)	4.25*
Total for all species combined	7.81(3)	4.23	5.99(2)	9.75*

\* Significantly different; - = less at the sites where adult males were observed.





## CONCLUDING DISCUSSION

All adults and some yearlings occupied home ranges, while other yearlings wandered; some of the latter settled during the summer, perhaps as they found suitable habitat and/or become mature. A few sedentary males of both ages showed movement from and return to their home ranges during the summer, perhaps wandering or following other birds. Young adults often showed movement over winter which older males did not. Replacement of lost males was usually by yearlings and young adults.

The few yearlings which showed display activity and association with females did so about equally over the spring and summer, while adult display and association with females was concentrated during the breeding period. Adults were more localized during the breeding period than over the rest of the summer, particularly in the evening when they performed display flights on small display areas. Territoriality was shown for adults and suggested for yearlings. Territoriality was thought to function in spacing males.

On the main study area, males occurred only in the lodgepole pine forest where they showed a generally clumped dispersion. As localized males occupied areas of denser habitat than that of the lodgepole pine forest generally, I suggested males utilized the denser habitat for food and shelter and that clumping was due to habitat



availability and selection. Adults utilized greater overstory cover and lower middlestory cover, while localized yearlings utilized greater middlestory cover than that of the resident areas generally. Wandering yearlings on the resident areas did not utilize significantly different habitat than on the resident areas generally, but wandering yearlings on the peripheral areas utilized greater overstory cover than on the peripheral areas generally. A display area, believed typical, had more open overstory cover and lower stem density than the habitat over the rest of the home ranges generally, perhaps facilitating display activity. During the moulting period as opposed to the breeding period, males utilized greater middlestory cover, perhaps as shelter during the moult. Adult males utilized habitat of greater overstory cover and lower middlestory cover than females.

If habitat availability and selection aggregate males and territorial behavior spaces them, I suggest the two factors interact to help form the patterns of spring and summer dispersion of male Franklin's grouse in the lodgepole pine forest of southwestern Alberta.



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## APPENDIX





Appendix 1. The cover values for the species of plants in the overstory and middle-story of 225 random samples of lodgepole pine forest.

Cover value*	Species										Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											
6											5
5		3									53
4		42									89
3		93									67
2	2	70	1	2	1						10
1	29	15	5	2	54						1
0	89		219	221	170						
	105	2									
Middlestory											
6											6
5											25
4											63
3	1		1		2	3			1	5	
2	5	3		2	16	10	2	1	32	14	
1	87	32	7	14	126	56	1	2	192	206	
0	132	190	217	209	81	124	222	222			

\*6 =>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 2. The cover values for the species of plants in the overstory and middle-story of 46 random samples of mixed forest.

Cover value*	Species							
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil
								Rose berry
								Total for all species combined
Overstory								
6								2
5				1				20
4		1		4	1			19
3	1	1	3	14	4			3
2	18	21	13	5	8			1
1	18	5	6	22				
0	9	18	24		33			
Middlestory								
6								5
5								27
4						4		13
3					1			1
2	3		1		15			
1	26	8	12	12	17	7	1	5
0	17	37	33	34	13	35	45	41
							2	38

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 3. The cover values for the species of plants in the overstory and middle-story of 17 random samples of white spruce forest.

Cover value*	Species							
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil
							Rose berry	Total for all species combined
Overstory								
6								1
5	1							4
4	3							7
3	8							5
2	4	1		1				
1			1	4				
0	1	16	16	16		13		
Middlestory								
6								
5								
4								
3								
2					5			6
1	5		1	2	6		1	9
0	12	17	16	15	6	17	16	2
							3	
							14	

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.





Appendix 4. The cover values for the species of plants of the middlestory of 22 random samples of meadow and marsh.

		Species								
Cover value*									Buffalo berry	Total for all species combined
		White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	
Middlestory	6									1
	5									6
	4					1		1		7
	3					4		2		1
	2	1			2	7	1			7
	1	1				2				1
	0	20	22		20	8	21	19	22	22

\*6=>95=100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 5. The cover values for the species of plants in the overstory and middle-story of 76 random samples from the resident areas.

Cover value*	Species										Total for all species combined
	White spruce	Lodge pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											
6											2
5		1									32
4		29									39
3		41									3
2		4									
1	5	1		1	26						
0	34		2	74	50						
	37		74								
Middlestory											
6											1
5											4
4						2					17
3						7					51
2	1	1			2					3	
1	37	7		5	56	18			14		
0	83	68		71	18	49	76	76	62	73	

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.







Appendix 7. The cover values for the species of plants in the overstory and middle-story at 227 sites where adult males were observed.

Cover value*	Species										
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	Total for all species combined
Overstory											
6											28
5		23									106
4		96									77
3		86		3							16
2		22		4							
1				10							
0			2	210							
			225								
Middlestory											
6											2
5											22
4											57
3				1					1		124
2		3		13							22
1		25		13					10		
0		199		213					216		
			3								
			224								
										</	

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.





Appendix 8. The cover values for the species of plants of the overstory and middle-story at 57 sites where localized males were observed.

Cover value*	Species							
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil
							Rose berry	Buffalo berry
								Total for all species combined
Overstory								
6								6
5		3		1				22
4		20						26
3		28						2
2	6	4		3	1			1
1	26	2		7	17			
0	25		6	46	39			
			51					
Middlestory								
6								1
5								2
4					2			7
3					3			
2	4	2			11	1	2	1
1	37	10		14	31	4	13	9
0	16	45		43	10	18	42	47
			56			34	51	

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.







Appendix 10. The cover values for the species of plants in the overstory and middlestory at 21 sites where wandering yearlings on the peripheral areas were observed.

Cover value*	Series										Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											
6											2
5		1									4
4		4									12
3		11									3
2	4	5			1						
1	9				4						
0	8		21	21	16						
Middlestory											
6											1
5											5
4						1					14
3						7				3	
2					12	13	12	21	21	18	
1	11	4			8						1
0	10	17	21	21							

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.





Appendix 11. The cover values for the species of plants in the overstory and middlestory of 10 random samples from a male's display area.

Cover value*	Species										Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											
6											2
5		1									6
4		7									2
3		2									
2											
1	4				1						
0	6		10	10	9						
Middlestory											
6											3
5										1	6
4										9	1
3											
2											
1	3	1			4	2					
0	7	9	10	10	6	6	10	10	10		

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 12. The cover values for the species of plants in the overstory and middlestory of 18 random samples from a male's home range excepting the display area.

Cover value*	Species								Total for all species combined	
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil		Rose berry
Overstory										
6										12
5		11								5
4		6								1
3		1								
2	2									
1	4				7					
0	12		18	18	11					
Middlestory										
6										2
5										2
4										12
3						1				
2					11	3			1	
1	7	2			6	14		18	17	
0	11	16	18	18			18			2

\*6=>95-100%, 5=>75-85%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 13. The cover values for the species of plants in the overstory and middlestory at 128 sites where adults were observed during the breeding period.

Cover value*	Species										Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											
6		11									23
5		49									46
4		53			4						47
3	1	13			14						12
2	3	2			35						
1	43		2	4	75						
0	81		126	124							
Middlestory											
6											
5											
4											
3					3	2					5
2	1	3			11	7			1		26
1	65	12		5	72	47		3	5		85
0	62	113	128	123	42	72	2	125	123	122	12

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 14. The cover values for the species of plants in the overstory and middlestory at 37 sites where adults were observed during the period of moult.

Cover value*	Species									Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	
Overstory										
6		3								3
5		18								21
4		11								11
3	1	5			2					2
2	5				8					
1	15									
0	16		37	37	27					
Middlestory										
6										1
5						2				10
4					13	8				19
3				1				1		
2	1			2	13	9			4	5
1	19	4	2		13				33	32
0	17	33	35	34	9	18	37	36		

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.





Appendix 15. The cover values for the species of plants of the overstory and middlestory at 215 sites where females were observed.

Cover value*	Species								Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	
Overstory									
6									21
5		6							68
4	1	45	1	1					82
3	3	74	3		3				38
2	27	61	6	1	16				6
1	83	19	12	13	43				
0	101	10	193	200	153				
Middlestory									
6					3				7
5					10				20
4					35	5	1		45
3					40	16	3	8	66
2	12	2	6	3	82	63	8	27	68
1	115	33	13	35	45	131	203	180	
0	88	180	196	177					9

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\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1=present-5%, 0=absent.



Appendix 16. The cover values for the species of plants of the overstory and middlestory at 80 sites where females were observed during the breeding period.

Cover value*	Species										Total for all species combined
	White spruce	Lodge-pole pine	Balsam poplar	Aspen	Willow	Alder	Dwarf birch	Shrubby cinquefoil	Rose berry	Buffalo berry	
Overstory											153
6		6									12
5		24									27
4	1	30			2						26
3	11	16	3	5	9						14
2	14	4	4	75	24						1
1	54		73	80	45						
0											
Middlestory											
6											6
5											28
4					3	1				2	44
3					11	6					
2	4				45	27	1	7	16	9	
1	41	8	2	5	21	46	79	73	64	69	
0	35	72	78	75							2

\*6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1-present-5%, 0=absent.











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